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Unisexual Lizards of the Genus *Gymnophthalmus* (Reptilia: Teiidae) in the Neotropics: Genetics, Origin, and Systematics

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CONTENTS

Abstract 2
Introduction 2
Acknowledgments 3
Methods 4
Morphological Characters 4
Univariate and Multivariate Analyses 5
Karyotypes 5
Biochemical Genetics 5
Reproduction 6
Results and Discussion 6
Did the Unisexual *G. underwoodi* Have a Hybrid Origin? 6
Does *G. underwoodi* Have a Clonal Pattern of Inheritance? 11
Who Are the Ancestors of *G. underwoodi* and Where Do They Occur? 11
Summary, Conclusions, and Scenario on the Hybrid Origin of *G. underwoodi* 24
References 25
Appendix—Specimens Examined 27

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ABSTRACT

Unisexual populations of *Gymnophthalmus underwoodi* occur in northern South America and the West Indies, primarily in open habitats where direct sunlight reaches the ground. Individual females from Suriname and from the main island of Trinidad have been shown to reproduce independently by parthenogenesis, and only female offspring are produced. Chromosomes and structural genes (detected by protein electrophoresis) reveal that inheritance is clonal in this diploid species, and the same clone occurs in Suriname and Trinidad. Individuals of *G. underwoodi* have enormous heterozygosity (45% of the 33 gene loci tested), indicating that this unisexual clone had a hybrid origin.

Two geographically and morphologically relevant bisexual species were investigated as the possible ancestors of *G. underwoodi*: *G. pleei* of Martinique, and *G. speciosus* of northern South America and neighboring islands. In addition, comparative electrophoretic data are presented for another more distantly related Neotropical microteiid, *Arthrosaura kockii*, from Suriname, because little is known about heterozygosity indices in bisexual microteiids to begin with.

Gymnophthalmus pleei is morphologically, karyotypically, and biochemically very distinct from the other *Gymnophthalmus* and is clearly ruled out as a possible ancestor of the unisexual species. However, we conclude that *G. speciosus* is one of the ancestors; it has a suite of chromosomes and structural genes that represent one of the two haploid genotypes detected in *G. underwoodi*, and its morphology is nearly identical to that of *underwoodi*.

The second bisexual ancestor of *G. underwoodi* remains to be found. We hypothesize that this ancestor occurs somewhere in or near the Guiana Region of South America (northern Brazil, eastern Venezuela, Guyana, Suriname, and French Guiana). The preferred habitat, external morphology, karyotype, and relative electrophoretic mobilities of proteins encoded by 33 gene loci are predicted for this unknown species, based on those described here for *underwoodi* and *speciosus*. These predictions can be tested by examining fresh samples from relevant populations.

Ecology and geographic distribution suggest that parthenogenesis in *Gymnophthalmus* had a hybrid origin in disturbed habitats, a pattern of origin similar to that of the unisexual lizards in the northern Temperate Zone. The hybridization probably occurred in northern South America, associated with shifts in distribution of savanna or other open habitats and forest. Such habitat shifts accompany fluctuations in rainfall, as in Pleistocene to Recent times, changes in the courses of rivers, and human modifications of natural habitats. Populations of *G. underwoodi* in the West Indies probably resulted from dispersal of the clone. Island colonization is particularly efficient in parthenogenetic species; reproductive potential is enormous, as every normal individual produces offspring independently.

INTRODUCTION

The genus *Gymnophthalmus* comprises six known species of lizards. It is among the three dozen Neotropical genera that often are referred to informally as "microteiids" and recently have been shifted back and forth between the families Teiidae and Gymnophthalmidae (e.g., Presch, 1983; Harris, 1985; several chapters in Estes and Pregill, 1988). Final assignment of these taxa at the familial level awaits a thorough review of all genera. Until such a review is completed, we continue to use Teiidae (sensu lato).

The range of *Gymnophthalmus* is from southern Mexico to Argentina (plus certain islands off northern South America and in the West Indies; Stuart, 1939; Peters and Donoso-Barros, 1970). One of the species, *Gymnophthalmus underwoodi* Grant, originally thought to occur only in the West Indies, is one of the few species of vertebrates with unisexual populations; Thomas (1965) reported that all known specimens were females. Hoogmoed (1973) later reported that *G. underwoodi* also occurs in Suriname and Guyana, and he brought the number of known specimens to nearly 100—all females.

The first males identified as *G. underwoodi* were discovered by Vanzolini (1976); he found four males among 22 apparent *underwoodi* specimens from Suriname and Brazil in the herpetological collection of the Museu de Zoologia, Universidade de Sao Paulo, Brazil. Additional males, from Colonia Coronel Mota, Roraima, northern Brazil, were reported by Cunha (1981). Vanzolini (1976) proposed that the occurrence of only a few

males in a few populations suggested that unisexuality is evolving in *G. underwoodi* now, and the males could be becoming extinct. This explanation seemed more reasonable than suggesting that the scarcity of males was due to a sampling artifact. In addition, the absence of morphological characters indicating hybrid traits in *G. underwoodi* suggested that all-female populations had a nonhybrid origin (Vanzolini, 1976). However, this is in contrast to the hybrid origins previously known for unisexual species of teiid lizards in the northern Temperate Zone (e.g., Lowe and Wright, 1966; Neaves, 1969; Parker and Selander, 1976; Cole et al., 1988; Dessauer and Cole, 1989), and more recently reported also for Neotropical species (Cole et al., 1983, 1989; Dessauer and Cole, 1989; Sites et al., 1990; Vyas et al., 1990).

To date, all but one of the most thoroughly investigated unisexual species of vertebrates has been shown conclusively to have had a hybrid origin (for reviews, see Cole, 1975; Darevsky et al., 1985; Dawley and Bogart, 1989). The one exception is the Neotropical xantusiid lizard of the genus *Lepidophyma* from Panama, for which a hybrid origin still is not completely ruled out (Bezy and Sites, 1987). Thus, the reports of a few males and lack of evidence for a hybrid origin of unisexual populations of *G. underwoodi* warranted further research (Cole et al., 1983, 1989).

Our first two questions were: (1) Do females of *G. underwoodi* from certain populations reproduce independently by parthenogenesis? (2) Are males of the same *G. underwoodi* produced in the laboratory or in nature? These questions were answered by collecting living *G. underwoodi* specimens in Trinidad and Suriname at localities from which no males were known and establishing laboratory colonies to study patterns of reproduction and reproductive histology. The colony females reproduced independently by parthenogenesis, generation after generation, and no males were identified (Hardy et al., 1989). Our next three questions, addressed in this report, are the following: (1) Did the unisexual *G. underwoodi* have a hybrid origin? (2) Does *G. underwoodi* have a clonal pattern of inheritance? (3) If *G. underwoodi* had a hybrid origin, who are its ancestors and where do they occur? In order to address these questions, we studied ecological, morphological, chromosomal, and biochemical characters of *G. underwoodi* from Trinidad and Suriname. These were compared with the same characters of freshly collected samples of two bisexual congeners from geographically relevant localities: *G. pleei* Bocourt (sample from Martinique) and *G. speciosus* (Hallowell) (sample from Chacachacare Island, Republic of Trinidad and Tobago, between the island of Trinidad and the Peninsula de Paria, Venezuela). In addition, we surveyed major herpetological collections and borrowed all preserved specimens of *G. underwoodi* from throughout its range, including the males reported by Vanzolini (1976) and by Cunha (1981), plus all specimens of *G. pleei* and all of *G. speciosus* from the Guiana Region. Morphological comparisons were also made with *G. lineatus* (Linnaeus), but the remaining two species, *G. multiscutatus* Amaral and *G. rubricauda* Boulenger are out of scope for this investigation morphologically and biogeographically (see below). In addition, comparative electrophoretic data are presented for another Neotropical microteiid lizard, *Arthrosaura kockii* (Van Lidth de Jeude), because little is currently known about heterozygosity indices in bisexual microteiids.

Acknowledgments

Permits and considerable assistance with logistics in the field were provided by S. A. J. Malone, F. L. J. Baal, and M. H. S. Miskin (Suriname Forest Service), Jean Chevance (Commissaire de la Republique de la Region Martinique), and Bheesham Ramdial and Bal Ramdial (Wildlife Section, Forestry Division, Republic of Trinidad and Tobago). Hans E. A. Boos, Curator of the Emperor Valley Zoo, Trinidad, was exceedingly helpful in the field, particularly in introducing us to Chacachacare Island and its fascinating fauna, including the bisexual population of *Gymnophthalmus*. Julius Boos initially identified *G. underwoodi* at Simla, Trinidad, for Grace M. Tilger and CRT in 1977, and those specimens were the foundation for this work. Important specimens and help were also provided by Jeffrey A. Cole, Ronald I. Crombie,

John de Bruin, Raymond A. Mendez, Tamara C. Minerly, Henry A. Reichart, and John Seyjagat, to whom we are most grateful. Marinus S. Hoogmoed (Nationaal Natuurhistorisch Museum, Leiden), who first discovered the unisexual populations in Suriname, has been most encouraging and helpful throughout this work.

Colleen C. Coogan and Mary E. Holden assisted with conscientious care and maintenance of the laboratory colony of *Gymnophthalmus*. Leslie F. Marcus, Gareth Nelson, and Steven J. Leipertz made available the microcomputer version of SAS. George F. Barrowclough continues to provide essential advice and guidance with computer programs and multivariate statistical analyses.

The abbreviations listed below are used throughout this report in reference to the specimens examined (more than 450; see Appendix). Most of these were borrowed from various herpetological collections, and we are grateful to our colleagues (in parentheses) who facilitated these loans.

AMNH	American Museum of Natural History, New York (George W. Foley)
ANSP	Academy of Natural Sciences, Philadelphia (Edmond V. Malnate)
ASFS	private collection of Albert Schwartz, Miami (collection presently at KU)
BMNH	British Museum (Natural History), London (Andrew F. Stimson)
CM	Carnegie Museum, Pittsburgh, Pennsylvania (Clarence J. McCoy)
FMNH	Field Museum of Natural History, Chicago, Illinois (Robert F. Inger; Hymen Marx)
KU	University of Kansas, Lawrence (William E. Duellman)
LACM	Natural History Museum of Los Angeles County, California (Robert L. Bezy; John W. Wright)
MCZ	Museum of Comparative Zoology, Harvard University (Pere Alberch; Jose P. Rosado)
MNHN	Museum National d'Histoire Naturelle, Paris (E. R..Brygoo)
MPEG	Museu Paraense Emilio Goeldi, Belem, Brazil (Teresa Cristina S. Avila Pires)
MR	collection of Mark O'Shea of Penn, Wolverhampton, W. Midlands, England
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley (Harry W. Greene)
MZUSP	Museu de Zoologia, Universidade de Sao Paulo, Brazil (Paulo Vanzolini)
RMNH	Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (Marinus S. Hoogmoed)
SDSNH	San Diego Society of Natural History, California (Gregory K. Pregill)
TCWC	Texas Cooperative Wildlife Collection, Texas A&M University, College Station (James R. Dixon)
UF	Florida State Museum, University of Florida, Gainesville (Walter Auffenberg)
UIMNH	University of Illinois Museum of Natural History, Urbana (Linda R. Maxson)
UMMZ	University of Michigan Museum of Zoology, Ann Arbor (Arnold G. Kluge)
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (George R. Zug; Ronald I. Crombie)

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METHODS

Morphological Characters

Color notes and photographs were taken in life for specimens we collected. Characters of external morphology were determined as de-

scribed by Hoogmoed (1973), but some require additional comment, as follows.

Sex was determined either by observation of everted hemipenes or dissection (inspection of hemipenes or gonads). Infralabial scales were counted from the mental posteriad to the posterior edge of the eye. Gular scales were counted beginning at the last enlarged genial scale on the right side posteriad to (but not including) the enlarged, midventral, triangular, pectoral scale. Ventral scales (right of midline) were counted from the same pectoral scale to (but not including) the enlarged, central (midventral) preanal scale. Subdigital lamellae on the fourth toe and third finger (fourth finger if treating the first as present) were counted from the claw (not included) to (but not onto) the foot or hand; if enlarged lamellae of this series extended onto the foot or hand, they were not counted.

Univariate and Multivariate Analyses

For univariate analyses and comparisons, reduced data are presented as the mean plus or minus one standard error of the mean. There was substantial concordance in variation among some morphological characters. These characters significantly covaried among the taxa, so each character should not be assumed to represent a completely independent estimate of the patterns of variation among these *Gymnophthalmus*. Therefore, multivariate combinations of the characters may represent better (nonredundant) estimates of the patterns of morphological variation. Consequently, we performed principal components analyses (PCA) of the morphological data, using the SAS program for microcomputers. (PCA in the Factor procedure, with PC scores standardized to unit variance.)

Ten characters were used for PCA: snout-vent length; number of femoral pores (total for both sides, table 3, except in analyses of females, which always lacked pores); and the number of the following epidermal scales: supralabials (total for both sides, table 3); infralabials (total for both sides, table 3); gulars; ventrals; dorsals; scales around midbody; subdigital lamellae on the fourth toe; and subdigital lamellae on the third finger. Only specimens with complete data in the matrix (no blank cells) were used. For toe lamellae, only the right foot was used in principal components analyses, but if the specified right toe was missing, the left foot was used. For finger lamellae, only the left hand was used in principal components analyses, but if the specified left finger was missing, the right hand was used. Given the number and combination of toes and fingers missing on certain specimens, this maximized the number of specimens used in the analyses and violated no assumptions, as Student's *t*-tests indicated no left-right asymmetry in counts of lamellae.

Karyotypes

Karyotypes were prepared and studied as described for other teiid lizards (Cole, 1979). The most productive tissue in tiny microteiids has been vertebral bone marrow, to which we usually added the spleen. We examined chromosomes of 137 mitotic and meiotic cells from 26 lizards (*G. underwoodi*, *G. pleei*, and *G. speciosus*).

Biochemical Genetics

Samples of fresh tissues (liver, heart, kidneys, stomach, small intestine, plasma, blood cells, and often the tail) were collected prior to preservation of adult and subadult lizards. For some juveniles and hatchlings, the entire lizard was frozen intact. *Gymnophthalmus* and *Arthrosaura* are so small that usually the samples of livēr, heart, and kidney from an individual were pooled prior to homogenization. Samples from different individuals were never pooled. Tissues were maintained in the frozen tissue collection at the Museum of Natural Science, Louisiana State University, Baton Rouge. Methods of tissue storage and curation have been described (Dessauer and Hafner, 1984; Dessauer et al., 1990).

Electrophoresis of tissue proteins of 80 lizards was conducted as described in detail for other teiids (Dessauer and Cole, 1990). Table 1 lists the buffers used, the loci examined, the enzyme commission numbers, and abbreviations recommended by Shaklee et al. (1989).

TABLE 1
Presumptive Structural Gene Loci Examined in *Gymnophthalmus* and *Arthrosaura*

Locus	EC no.	Abbrev.[a]	Buffer[b]
Oxidoreductases			
Alcohol dehydrogenase	1.1.1.1	ADH	TM, 7.4, NAD, EDTA, Mg
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G3PDH	PC, 6.0
L-Lactate dehydrogenase	1.1.1.27	LDH-1	TM, 7.4
		LDH-2	
Malate dehydrogenase	1.1.1.37	sMDH	PC, 6.0
		mMDH	
Isocitrate dehydrogenase	1.1.1.42	sIDHP	TM, 7.4, NADP, EDTA, Mg
		mIDHP	
Phosphogluconate dehydrogenase	1.1.1.44	PGDH	TM, 7.4, NADP, EDTA, Mg
Superoxide dismutase	1.15.1.1	sSOD	TM, 7.4
		mSOD	
Transferases			
Aspartate aminotransferase	2.6.1.1	sAAT	TM, 7.4
		mAAT	
Alanine aminotransferase	2.6.1.2	ALAT	TM, 7.4
Pyruvate kinase	2.7.1.40	PK	TM, 7.4
Creatine kinase	2.7.3.2	CK-1	TM, 7.4
		CK-2	
Adenylate kinase	2.7.4.3	AK	TM, 7.4
Hydrolases			
Esterase D	3.1.1.–	ESTD[c,d]	PC, 6.0; TM, 7.4
Acid phosphatase	3.1.3.2	ACP[e]	PC, 6.0
Dipeptidase	3.4.–.–	PEPA[f]	TM, 7.4
Tripeptide aminopeptidase	3.4.–.–	PEPB[g]	PC, 6.0
Peptidase-C	3.4.–.–	PEPC[h]	PC, 7.4
Tripeptidase-E	3.4.–.–	PEPE[g]	PC, 6.0
Proline dipeptidase	3.4.13.9	PEPD[i]	TM, 7.4
Adenosine deaminase	3.5.4.4	ADA	TM, 7.4
Lyases			
Aconitate hydratase	4.2.1.3	sAH	TC, 7.4
		mAH	
Isomerases			
Mannose-6-phosphate	5.3.1.8	MPI	TM, 7.4
Glucose-6-phosphate	5.3.1.9	GPI	PC, 6.0
Phosphoglucomutase	5.4.2.2	PGM	PC, 6.0
Nonenzymic blood proteins			
Transferrin		TF	V, 8.6
Albumin		ALB	V, 8.6

[a] Shaklee et al. (1989); s = cytosolic enzyme; m = mitochondrial enzyme.
[b] Buffer components, pH, and additives: C = citric acid; M = maleic acid; P = disodium hydrogen phosphate; V = veronal (barbituric acid).
[c] Substrate 4-methylumbelliferyl acetate.
[d] Inactive with alpha-naphthyl esters.
[e] Substrate 4-methylumbelliferyl phosphate.
[f] Substrate phenylalanyl.leucine.
[g] Substrate leucyl.glycyl.glycine.
[h] Substrate lysyl.leucine.
[i] Substrate phenylalanyl.proline.

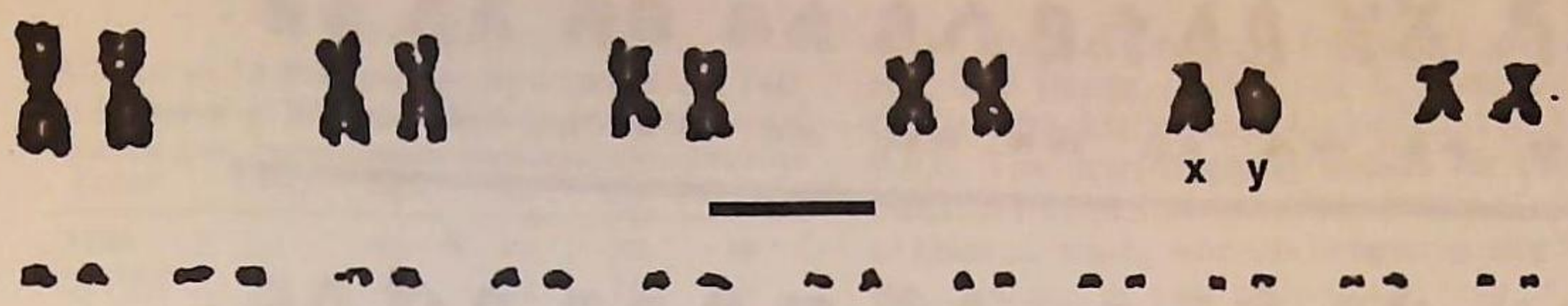


Fig. 1. Diploid karyotype of the bisexual *Gymnophthalmus pleei* ($2n = 34$, AMNH 128430, male). The fifth largest pair of chromosomes is heteromorphic; females have XX. Bar represents 10 μ.

Reproduction

Procedures for maintaining captive *Gymnophthalmus* in reproducing lineages have been detailed elsewhere (Townsend and Cole, 1985; Hardy et al., 1989).

RESULTS AND DISCUSSION

Did the Unisexual G. underwoodi *Have a Hybrid Origin?*

We hypothesized that if *G. underwoodi* had a hybrid origin, its karyotype might consist of two or more distinct haploid complements of chromosomes, as in some other unisexual species (e.g., *Cnemidophorus neomexicanus*; Lowe and Wright, 1966; Cole et al., 1988). We also predicted that electrophoresis of tissue proteins would reveal that *G. underwoodi* has a high degree of heterozygosity (probably at least 20% of the gene loci tested), whereas if it had a nonhybrid origin, heterozygosity would be low (10% or less), as found in comparable *Cnemidophorus* species (Neaves, 1969; Parker and Selander, 1976; Dessauer and Cole, 1984, 1989; Cole et al., 1983, 1988). In addition, we predicted that if *G. underwoodi* had a hybrid origin, comparative investigations with geographically relevant samples of bisexual species of *Gymnophthalmus* would reveal its ancestors.

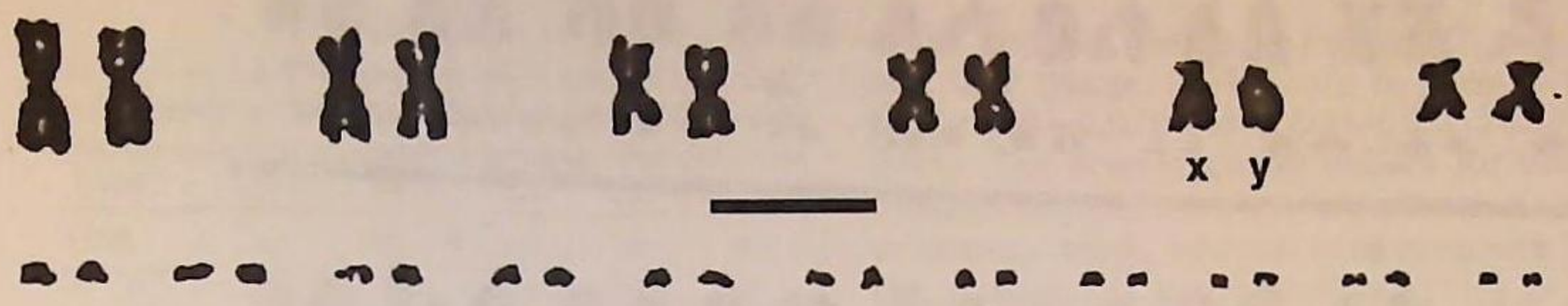
A review of all known species of *Gymnophthalmus* suggested that the bisexual ancestors of *G. underwoodi* could well be represented by *G. speciosus* of northern South America (or Chacachacare Island, Republic of Trinidad and Tobago), and either *G. pleei* of Martinique or some other little known (Vanzolini, 1976; Cunha, 1981) or unknown bisexual populations of *Gymnophthalmus* in northern South America. Consequently, we collected samples from relevant localities and compared their chromosomes and proteins. In addition, we compared these lizards in preferred habitat and external morphology (color, color pattern, size, scutellation; see below).

Karyotypes

We compared karyotypes of the following species: *Gymnophthalmus pleei* (Martinique; 3 males, 2 females; 36 cells); *G. speciosus* (Chacachacare Island, Republic of Trinidad and Tobago; 4 males, 1 female; 38 cells); and *G. underwoodi* (St. Augustin, Trinidad; Brokopondo and Christiaankondre, Suriname; 16 females; 63 cells).

Gymnophthalmus pleei has a distinctive karyotype with the lowest number of chromosomes known in microteiids (fig. 1). The diploid number is 34, with 12 larger macrochromosomes (all biarmed) and 22 microchromosomes (with up to 4 biarmed in the clearest cells). The macrochromosomes of the females appear as follows: the largest four pairs, all metacentric; fifth largest pair, subtelocentric; sixth pair, submetacentric. The males were identical, except consistently the fifth largest pair was heteromorphic, with one subtelocentric as in the females plus one telocentric (fig. 1). Thus, we conclude that *G. pleei* has an XY (♂):XX (♀) sex chromosome system. No consistent secondary constrictions were observed.

In sharp contrast, *G. speciosus* has a much larger number of chromosomes, including several pairs of telocentric macrochromosomes (fig. 2, top). Its diploid number is 44, with 20 macrochromosomes and 24 microchromosomes (up to 6 biarmed in the clearest cells). Males and females are apparently iden-



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In sharp contrast, *G. speciosus* has a much larger number of chromosomes, including several pairs of telocentric macrochromosomes (fig. 2, top). Its diploid number is 44, with 20 macrochromosomes and 24 microchromosomes (up to 6 biarmed in the clearest cells). Males and females are apparently iden-

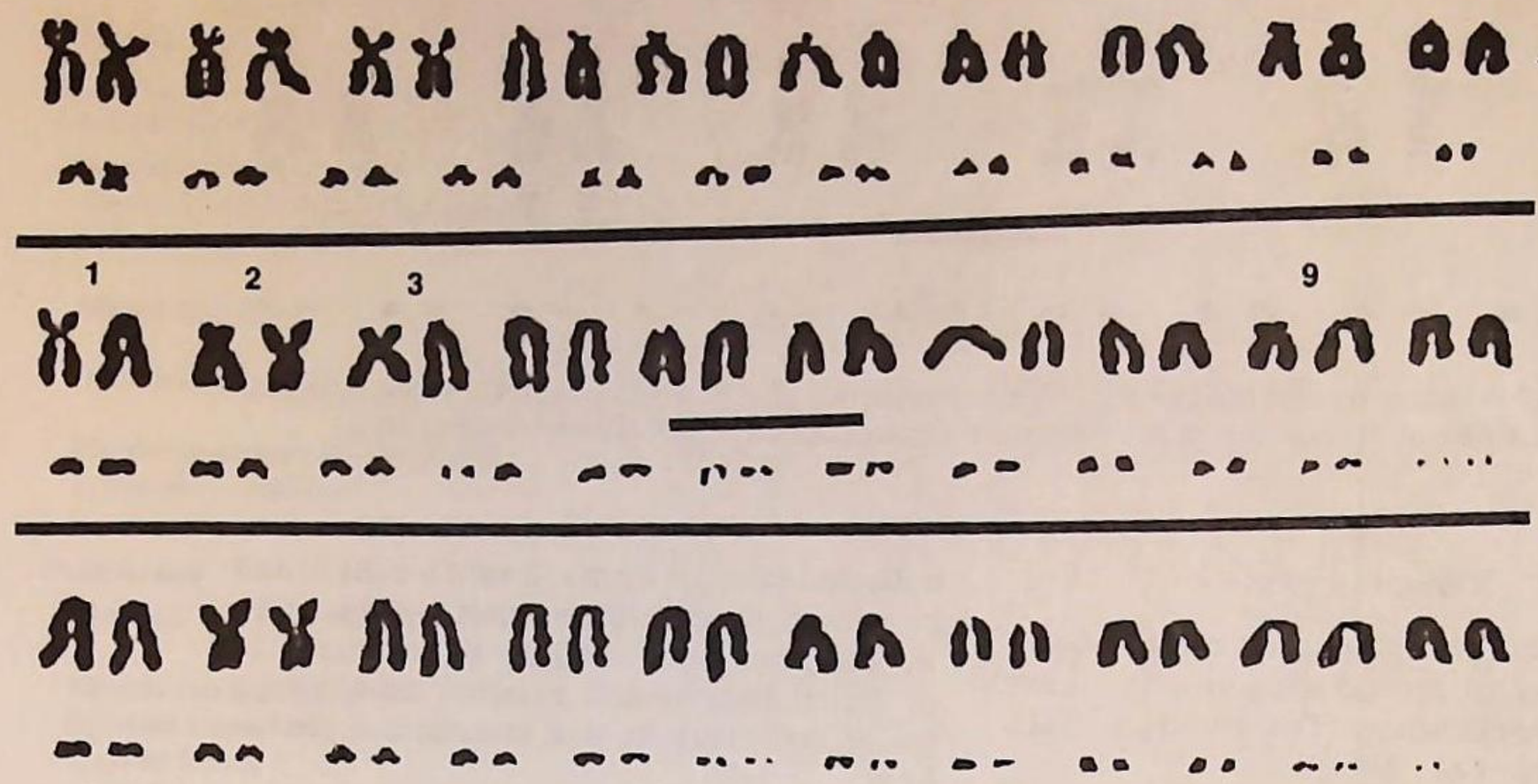

Fig. 2. Diploid karyotypes of three species of *Gymnophthalmus* (in each, $2n = 44$), two real and one hypothetical. **TOP**, the bisexual *G. speciosus* (AMNH 128440, male). The first, second, third, and ninth pairs of macrochromosomes are submetacentric or clearly subtelocentric, whereas the rest are telocentric or essentially so. **MIDDLE,** the unisexual *G. underwoodi* (AMNH 133314, female). The left chromosome of each pair matches a haploid set from *G. speciosus,* in this interpretation with four heteromorphic pairs (1, 2, 3, 9). Line represents 10 μ. **BOTTOM**, hypothetical diploid karyotype of the second bisexual ancestor of *G. underwoodi.* Using two prints of the cell from *underwoodi,* we took the right chromosome of each pair twice (middle karyotype). We predict that the 33 proteins for *G.* ??? shown in table 2 will be found in lizards having a karyotype identical or very similar to this.

tical, with no morphologically recognizable sex chromosomes. The macrochromosomes appear as follows: the largest three pairs, all submetacentric; the fourth through eighth plus tenth largest pairs, all telocentric; and the ninth pair, submetacentric to subtelocentric. No secondary constrictions were observed.

The karyotype of *G. underwoodi* is vastly different from that of *G. pleei* but in some respects is very similar to that of *G. speciosus.* Indeed, the diploid karyotype of *underwoodi* appears to include a perfect, complete haploid complement of chromosomes from *speciosus* (fig. 2, middle). As in *G. speciosus,* there are 44 chromosomes in *G. underwoodi,* with 20 macrochromosomes and 24 microchromosomes (up to 6 biarmed in the clearest cells). The macrochromosomes show considerable heteromorphism: There are 15 telocentrics; three among the largest six chromosomes are submetacentric, similar to those in *speciosus*; one among the largest six is metacentric, unlike any in *speciosus*; and one among the smallest is submetacentric to subtelocentric, similar to one in *speciosus* (pair 9). Because one haploid set matches perfectly that of *G. speciosus* (fig. 2), we hypothesize that the other haploid set represents the karyotype (fig. 2, bottom) of the other bisexual species that hybridized with *G. speciosus* in the ancestry of *G. underwoodi.*

Biochemical Genetics

Proteins encoded by 33 presumptive structural gene loci were compared by electrophoresis in *G. underwoodi* (N = 67 compared), *G. speciosus* (N = 6), *G. pleei* (N = 5), and *Arthrosaura kockii* (N = 2; table 2; fig. 3). As predicted, mean heterozygosity was high in the unisexual *G. underwoodi*; 15 out of 33 loci (H = 0.45). Five of these heterozygous patterns are shown in figure 3. In contrast, mean heterozygosity was below 0.10 for each

TABLE 2

Alleles[a] at 33 Presumptive Structural Gene Loci in Samples[b] of *Gymnophthalmus* and *Arthrosaura*

Locus[c]	UND	SPE	???	PLE	ART
ADH	ac	cc	aa	bb	bb
G3PDH	bb	bb	bb	bb	aa
LDH-1	aa	aa	aa	bb	cc
LDH-2	bb	bb	bb	bb	aa
sMDH	aa	aa	aa	aa	ab[d]
mMDH	ac	cc	aa	cc	bb
sIDHP	aa	aa	aa	bb	cc
mIDHP	aa	aa	aa	aa	bb
PGDH	ab	bb	aa	bb	cc
sSOD	aa	aa	aa	cc	bb
mSOD	aa	aa	aa	aa	bb
sAAT	ac	aa	cc	aa	bb
mAAT	bb	bb	bb	bb	aa
ALAT	bc	ba[e]	cc	ab[f]	cc
PK	aa	aa	aa	bb	aa
CK-1	bb	bb	bb	bc[g]	aa
CK-2	cc	cc	cc	ba[h]	dd
AK	aa	aa	aa	aa	aa
ESTD	cc	cc	cc	bb	aa
ACP	ab	aa	bb	ab[i]	cc
PEPA	cc	cb[j]	cc	cc	aa
PEPB	ab	aa	bb	aa	bb
PEPC	bc	cc	bb	aa	aa
PEPE	bb	bb	bb	bb	aa
PEPD	de	cdb[k]	ee	bb	aa
ADA	ab	bb	aa	ba[l]	cc
sAH	cd	de[m]	cc	bb	aa
mAH	bb	bb	bb	bb	aa
MPI	ac	ca[n]	ac	aa	bb
GPI	ac	cad[o]	ac	bb	ee
PGM	bc	cb[p]	bc	cc	aa
TF	ab	bb	aa	bb	cc
ALB	aa	aa	aa	bb	aa

[a] Alleles are designated in alphabetical sequence in order of decreasing anodal migration. Polymorphism was fixed in *G. underwoodi*. For all other species, alleles are listed in order of frequency (highest to lowest) for polymorphic loci.

[b] UND = *G. underwoodi*, 12 specimens from two sites in Trinidad plus 33 specimens from three sites in Suriname plus 22 specimens of Suriname stock representing the F_1 through F_3 generations reared in the laboratory. SPE = *G. speciosus*, 6 specimens from Chacachacare Island, Republic of Trinidad and Tobago. ??? = unknown bisexual ancestor that hybridized with *G. speciosus* and gave rise to *G. underwoodi*; alleles for ??? are predicted; all others in this table were determined experimentally. PLE = *G. pleei*, 5 specimens from one site in Martinique. ART = *A. kockii*, two specimens from one site in Suriname.

[c] For multilocus systems, loci are numbered in order of decreasing anodal migration of their polypeptide products.

[d] Frequency of a = 0.75; b = 0.25.

[e] Frequency of b = 0.75; a = 0.25.

[f] Frequency of a = 0.70; b = 0.30.

[g] Frequency of b = 0.80; c = 0.20.

[h] Frequency of b = 0.70; a = 0.30.

[i] Frequency of a = 0.90; b = 0.10.

[j] Frequency of c = 0.92; b = 0.08.

[k] Frequency of c = 0.67; d = 0.25; b = 0.08.

[l] Frequency of b = 0.90; a = 0.10.

[m] Frequency of d = 0.92; e = 0.08.

[n] Frequency of c = 0.75; a = 0.25.

[o] Frequency of c = 0.83; a = 0.085; d = 0.085.

[p] Frequency of c = 0.90; b = 0.10.

of the bisexual species, as follows: *G. speciosus*, 0.07 (range, 0.03–0.10); *G. pleei*, 0.05 (range, 0.03–0.07); and *A. kockii*, 0.015 (0.00–0.03). The heterozygosity indices for these bisexual microteiids are close to those of other bisexual teiids, whereas heterozygosity for the unisexual *G. underwoodi* is as high as or higher than that of most other unisexual teiids (e.g., Parker and Selander, 1976; Dessauer and Cole, 1984, 1989). This is consistent with the hypothesis that *G. underwoodi* had a hybrid origin.

For 12 (36%) of the 33 loci tested, neither of the alleles present in *G. underwoodi* was detected in *G. pleei*, nor were the alleles for 27 (82%) of the 33 loci in *A. kockii*. Therefore, these two species are ruled out as ancestors for the unisexual species. In contrast, for all 33 loci tested, one complete haploid set of alleles in *G. underwoodi* was identical to a typical haploid set of *G. speciosus* (table 2). Thus, we conclude that *G. speciosus* is one of the two bisexual ancestors of the unisexual *G. underwoodi*. By the process of eliminating the known haploid genome of *speciosus* from the diploid genomes of *G. underwoodi*, we derive a prediction of the haploid genome contributed by the other ancestor and double that to represent a possibly typical diploid condition for that unknown species (table 2; ???).

As discussed below, *G. underwoodi* is very similar in external morphology to *G. speciosus* and probably also to its other bisexual

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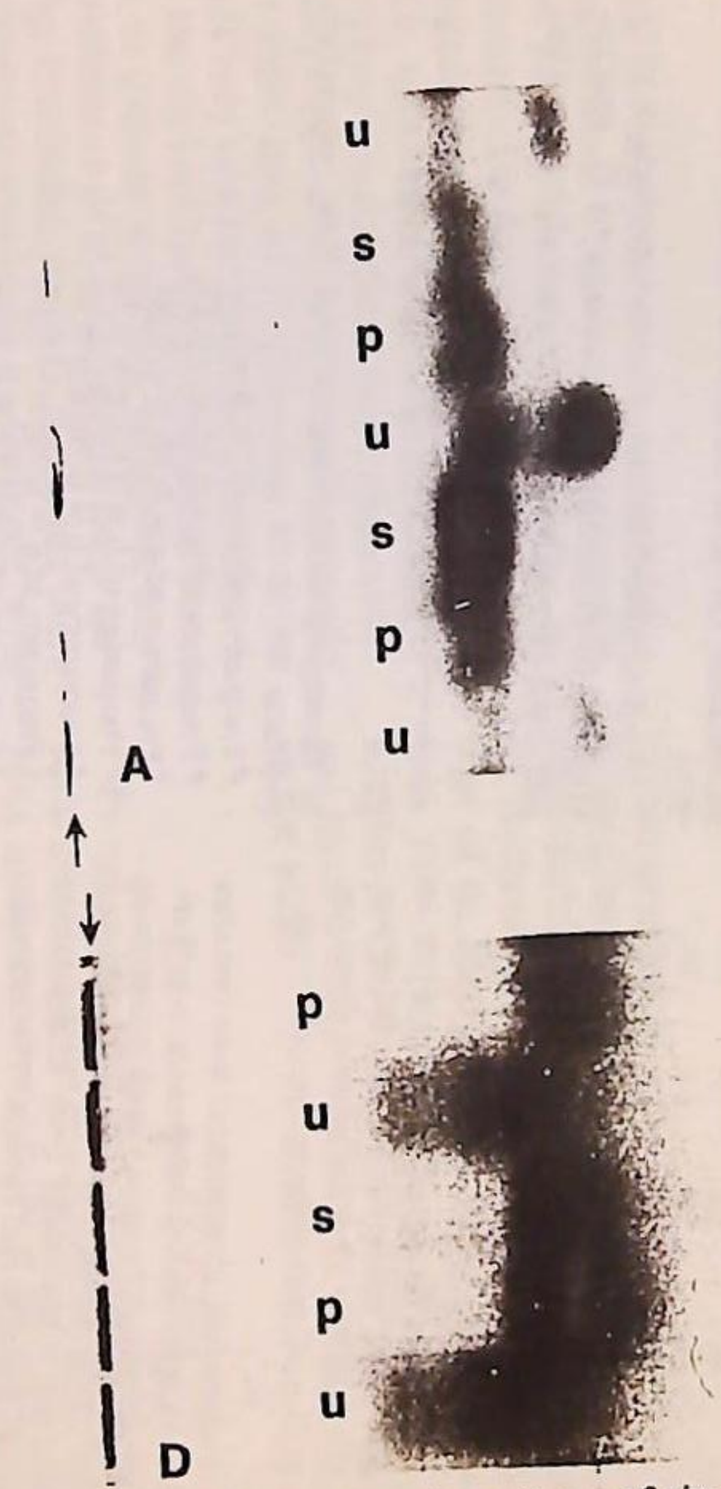

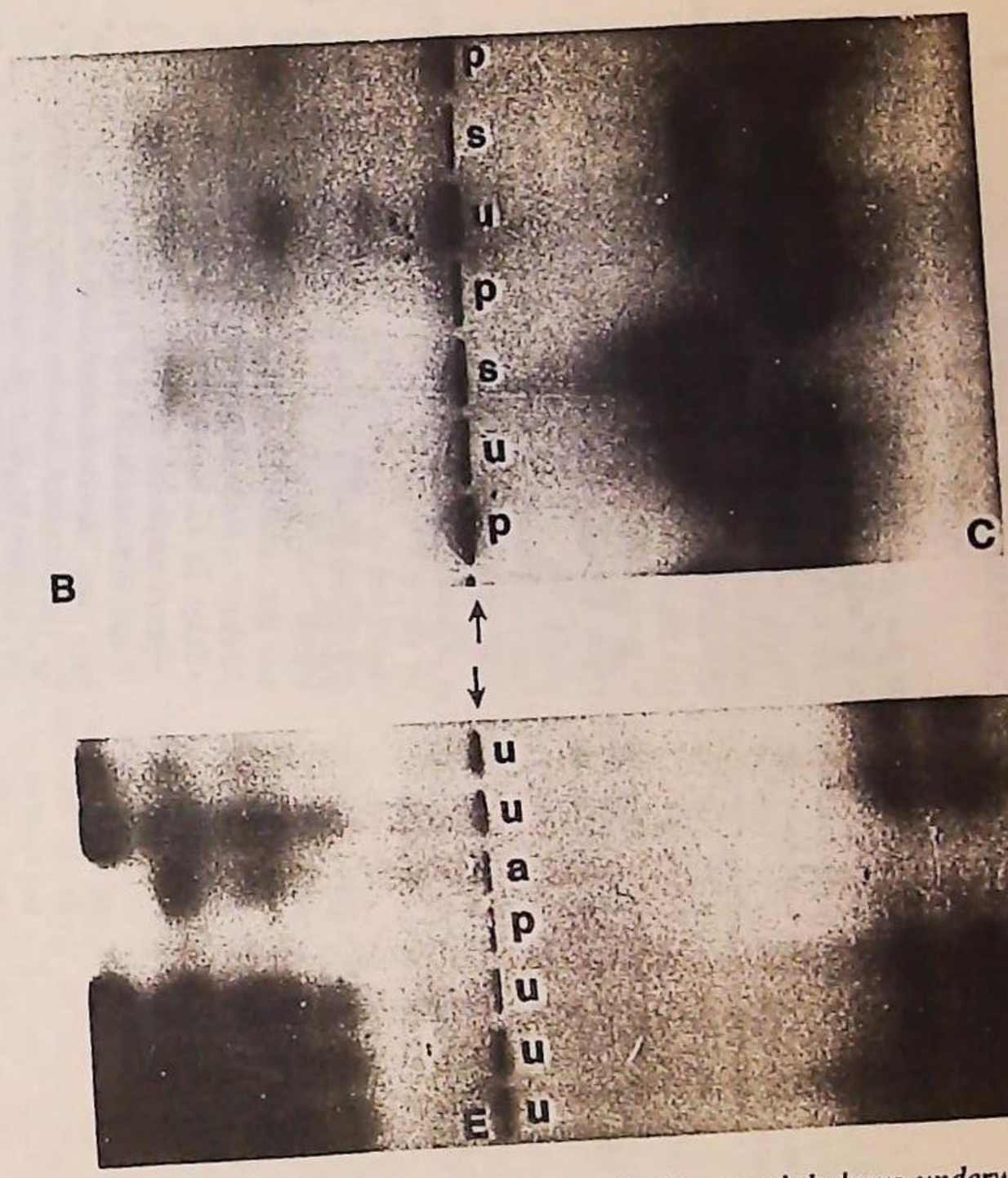

Fig. 3. Electrophoretic patterns of six enzymes, five of which indicate heterozygous genotypes in *Gymnophthalmus underwoodi* (cor
with table 2). **A.** PGM, seven specimens. **B.** ADH, seven specimens; these allozyme patterns appear on gels stained for PGM and MPI a
as for ADH. **C.** MPI, seven specimens; note that *G. speciosus* (s) is polymorphic at this locus. **D.** sAAT, five specimens. **E.** mAH, seven speci
F. sAH, seven specimens. Abbreviations: a, *Arthrosaura kockii*; p, *G. pleei*; s, *G. speciosus*; and u, *G. underwoodi*. Anode is to the right; a
indicate positions of sample applications.

ancestor. We suggest that at least three cryptic species are involved in this *underwoodi* complex. Genetically, however, the bisexual ancestors appear to be quite different (figs. 2, 3; table 2). In order to understand the genetic differences in the context of other lizards with which we are familiar, we compared the electrophoretic data for *G. underwoodi* with that for another diploid unisexual teiid of hybrid origin, *Cnemidophorus neomexicanus*, which we have also analyzed (Cole et al., 1988). Our data sets for *G. underwoodi* and *C. neomexicanus* include 29 loci analyzed in both investigations. Of these, 13 (45%) bear alleles in the heterozygous state in *C. neomexicanus*, 12 (41%) are heterozygous in *G. underwoodi*. The bisexual ancestors of *C. neomexicanus* (*C. tigris marmoratus* and *C. inornatus*) are morphologically, ecologically, and karyotypically very distinct and sympatric at several ecotonal localities without evidence of interbreeding today (Cole et al., 1988). The ancestors of the unisexual *G. underwoodi* appear to be cryptic species that are as genetically distinct as the ancestors of the unisexual *C. neomexicanus*.

The 12 specimens of *Gymnophthalmus underwoodi* from two sites in Trinidad were identical in genotype to each other and to the 33 specimens from three sites in Suriname (table 2). This suggests that they represent the same clone (see below) and they share a common origin. We agree with Hoogmoed's (1973) conclusion that the populations of Trinidad and those of the Guiana Region represent one taxon, *G. underwoodi*.

Does G. underwoodi *Have a Clonal Pattern of Inheritance?*

The electrophoretic data for 32 (albumin was not recorded) of the 33 gene loci (table 2) include nearly complete observations on 25 specimens of Suriname stock (from Brokopondo), representing the following generations of three lineages reared in the laboratory: P_1 (N = 3 lizards), F_1 (N = 12), F_2 (N = 4), and F_3 (N = 6). All individuals were identical, even at the 15 loci that bear alleles in the heterozygous state. No effects of recombination or random assortment were observed. As in the parthenogenetic species of *Cnemidophorus* (Dessauer and Cole, 1986), the heterozygosity observed in *G. underwoodi* is fixed; inheritance is clonal. This is consistent with parthenogenesis as the mode of reproduction recently documented for *G. underwoodi* (Hardy et al., 1989).

Who Are the Ancestors of G. underwoodi *and Where Do They Occur?*

The karyotypic and electrophoretic data discussed above demonstrate that *G. underwoodi* had a hybrid origin, and they eliminate *G. pleei* from further consideration as one of its ancestors. In addition, the data strongly implicate *speciosus* as being one of the ancestors, so the next problem is to identify the second bisexual ancestor.

A review of the morphology of all six known species of *Gymnophthalmus* does not reveal a likely candidate for this missing ancestor, suggesting that it may be either extinct or yet to be recognized. The morphological data suggest that the unknown ancestor is exceedingly similar to *G. speciosus* and *G. underwoodi*.

Univariate Morphological Analyses

Relatively variable body measurement and epidermal scale count data are presented for 10 characters in table 3. We also recorded data on numerous additional characters that provided no differences for distinguishing among any of the samples of *G. speciosus*, *G. underwoodi*, *G. pleei*, and *G. lineatus* compared (with few exceptions noted in the following list). Thus, these species share the following characters with insignificant variation: prefrontals paired, contacting each other at median suture; frontonasal separated from first supraciliary by prefrontals; one supraocular; no frontoparietals; nasal entire; nare about central in, or a bit below, center of nasal (but low in nasal of *G. pleei*); one loreal; one frenocular; one preocular; one subocular; three postoculars (uppermost smallest); three anterior plus two posterior temporals; two supraciliaries (posterior one very small); cephalic scales smooth; one postmental; two pairs enlarged genials; preanals usually one large central, three posterior edging cloaca, two very small laterals each side; dorsal body scales smooth (but keeled on posterior body

External Morphological Data[a] for 23 Samples (Four Species?) of *Gymnophthalmus*

Species	Sample	Sex	Body length	Supralabials	Infralabials	Gulars	Ventrals
G. underwoodi	Barbados; A	♀	32.6 ± 0.80 (20–41) 38	16.0 ± 0.02 (16–17) 40	8.0 ± 0.02 (8–9) 40	9.4 ± 0.09 (9–11) 40	22.4 ± 0.10 (21–23) 38
G. underwoodi	Guadelupe; N	♀	31.5 ± 1.36 (19–41) 23	16.0 ± 0.00 (16–16) 22	8.0 ± 0.04 (8–9) 22	9.3 ± 0.10 (9–10) 22	22.4 ± 0.14 (21–24) 23
G. underwoodi	Dominica; O	♀	29.7 (26–34) 6	16.0 (16–16) 6	8.0 (8–8) 6	8.8 (8–9) 6	22.0 (20–23) 6
G. underwoodi	St. Vincent Island; B	♀	34.0 ± 0.94 (24–41) 27	16.0 ± 0.00 (16–16) 27	8.0 ± 0.04 (8–9) 27	9.3 ± 0.10 (9–10) 23	22.5 ± 0.11 (22–23) 22
G. underwoodi	Grenada; C	♀	30.5 (25–36) 2	16.0 (16–16) 2	8.0 (8–8) 2	9.0 (9–9) 2	22 (–) 1
G. underwoodi	Trinidad; D	♀	34.7 ± 0.68 (21–41) 49	16.0 ± 0.00 (16–16) 49	8.1 ± 0.04 (7–9) 49	9.5 ± 0.07 (9–10) 47	22.4 ± 0.11 (21–24) 47
G. underwoodi	Guyana (north.); E	♀	33.1 ± 1.14 (17–40) 30	16.0 ± 0.00 (16–16) 30	8.1 ± 0.05 (8–9) 30	9.7 ± 0.08 (9–10) 30	23.1 ± 0.15 (21–24) 28
G. underwoodi?[b]	Guyana (east.); F	♀	37 (–) 1	16 (–) 1	8 (–) 1	10 (–) 1	24 (–) 1
G. underwoodi	French Guiana; G	♀	26.5 (20–33) 2	16.0 (16–16) 2	8.0 (8–8) 2	†0.0 (10–10) 2	23 (–) 1
G. underwoodi	Suriname (north.); H	♀	32.7 ± 2.06 (17–41) 12	16.0 ± 0.00 (16–16) 12	8.1 ± 0.08 (8–9) 12	9.4 ± 0.15 (9–10) 12	22.5 ± 0.29 (21–24) 12
G. underwoodi?[b]	Suriname (south.); I	♀	21 (–) 1	16 (–) 1	8 (–) 1	9 (–) 1	—
G. underwoodi	Suriname (Broko.); J	♀	31.1 ± 1.78 (20–40) 12	16.1 ± 0.08 (16–17) 12	8.1 ± 0.08 (8–9) 12	9.4 ± 0.16 (9–10) 10	22.6 ± 0.16 (22–23) 10
G. underwoodi?[b]	Suriname (Voltz.); K	?	23 (–) 1	16 (–) 1	8 (–) 1	9 (–) 1	22 (–) 1
G. underwoodi	Suriname (east.); L	♀	37.4 ± 0.60 (31–40) 17	16.0 ± 0.00 (16–16) 17	8.1 ± 0.06 (8–9) 17	9.4 ± 0.12 (9–10) 17	22.6 ± 0.21 (21–24) 17
G.?	Suriname (east.); Z	♀	36.0 ± 0.93 (31–41) 11	16.0 ± 0.00 (16–16) 11	8.0 ± 0.00 (8–8) 11	9.4 ± 0.15 (9–10) 17	22.5 ± 0.41 (21–26) 11
G. speciosus	Suriname (east.); P	♂	32.5 (32–33) 2	16.0 (16–16) 2	8.0 (8–8) 2	10.0 (10–10) 2	22.0 (22–22) 2
G. underwoodi ?	Brazil (Maracá); M	♀	40.0 (37–43) 8	15.9 (15–16) 8	6.0 (6–6) 8	9.0 (9–9) 8	22.2 (22–23) 8
G.?	Brazil; Q	♀	35.3 (30–40) 3	15.7 (15–16) 3	6.0 (6–6) 3	9.0 (9–9) 3	22.3 (22–23) 3
G. speciosus	Brazil; Q	♂	34.5 (32–37) 2	16.0 (16–16) 2	7.0 (6–8) 2	9.5 (9–10) 2	22.5 (21–24) 2
G. speciosus	Brazil (Mota); R	♀	34.3 ± 0.71 (30–39) 12	15.9 ± 0.08 (15–16) 12	8.0 ± 0.00 (8–8) 12	9.3 ± 0.19 (9–11) 12	25.4 ± 0.23 (24–27) 12
G. speciosus	Brazil (Mota); R	♂	31.9 ± 0.65 (28–35) 11	15.9 ± 0.16 (15–17) 11	8.0 ± 0.00 (8–8)) 11	9.6 ± 0.15 (9–10) 11	22.6 ± 0.34 (21–25) 11
G. speciosus	Guyana (south.); S	♀	31.7 (25–38) 6	15.8 (15–16) 6	7.8 (7–8) 6	9.7 (9–10) 6	25.5 (24–28) 4
G. speciosus	Guyana (south.); S	♂	32.4 (25–36) 5	16.0 (16–16) 5	8.0 (8–8) 5	10.2 (10–11) 5	23.5 (22–24) 4
G. speciosus	Trinidad; T	♀	33.8 (29–38) 5	16.0 (16–16) 5	7.8 (7–8) 5	9.2 (9–10) 5	25.0 (22–27) 5

TABLE 3
Extended

Dorsals	Scales around midbody	Left toe lamellae	Right toe lamellae	Left finger lamellae	Right finger lamellae	Femoral pores
33.2 ± 0.09 (32–34) 38	13.0 ± 0.00 (13–13) 39	16.9 ± 0.09 (16–18) 36	16.9 ± 0.10 (16–19) 32	12.9 ± 0.06 (12–13) 34	12.8 ± 0.08 (12–13) 33	0.0 ± 0.00 (0–0) 40
33.1 ± 0.12 (32–34) 22	13.0 ± 0.00 (13–13) 23	17.0 ± 0.12 (16–18) 21	16.9 ± 0.10 (16–18) 20	13.0 ± 0.08 (12–14) 22	12.9 ± 0.10 (12–14) 22	0.0 ± 0.00 (0–0) 23
32.7 (32–33) 6	13.0 (13–13) 6	17.2 (16–18) 4	17.4 (17–18) 5	13.0 (13–13) 6	12.8 (12–13) 6	0.0 (0–0) 6
32.9 ± 0.13 (32–34) 25	13.0 ± 0.00 (13–13) 26	17.1 ± 0.09 (16–18) 23	17.0 ± 0.09 (16–18) 25	13.0 ± 0.06 (12–14) 27	12.9 ± 0.10 (12–14) 24	0.0 ± 0.00 (0–0) 27
33.5 (32–35) 2	13.0 (13–13) 2	16.5 (16–17) 2	17.5 (17–18) 2	13.0 (13–13) 2	13.0 (13–13) 2	0.0 (0–0) 2
33.0 ± 0.09 (32–34) 46	13.0 ± 0.00 (13–13) 49	17.0 ± 0.10 (16–18) 44	16.9 ± 0.06 (16–18) 45	12.8 ± 0.07 (12–14) 44	12.6 ± 0.08 (11–13) 44	0.0 ± 0.00 (0–0) 47
33.3 ± 0.13 (32–35) 29	13.0 ± 0.00 (13–13) 30	17.0 ± 0.06 (16–18) 29	16.9 ± 0.10 (16–18) 28	12.8 ± 0.11 (11–14) 28	12.6 ± 0.13 (11–13) 29	0.0 ± 0.00 (0–0) 29
34 (–) 1	13 (–) 1	15 (–) 1	15 (–) 1	11 (–) 1	12 (–) 1	0 (–) 1
34.0 (34–34) 2	13.0 (13–13) 2	16.5 (16–17) 2	16.0 (16–16) 2	12.0 (12–12) 2	12.0 (12–12) 2	0.0 (0–0) 2
33.8 ± 0.24 (33–35) 12	13.0 ± 0.00 (13–13) 12	17.3 ± 0.14 (17–18) 11	17.1 ± 0.21 (16–18) 11	13.0 ± 0.21 (12–14) 10	12.8 ± 0.25 (12–14) 10	0.0 ± 0.00 (0–0) 12
33 (–) 1	13 (–) 1	16 (–) 1	17 (–) 1	13 (–) 1	12 (–) 1	0 (–) 1
33.9 ± 0.31 (33–36) 10	13.0 ± 0.00 (13–13) 11	17.0 ± 0.19 (16–18) 11	17.3 ± 0.14 (17–18) 11	12.8 ± 0.18 (12–14) 12	13.1 ± 0.19 (12–14) 12	0.0 ± 0.00 (0–0) 11
35 (–) 1	13 (–) 1	16 (–) 1	15 (–) 1	12 (–) 1	11 (–) 1	0 (–) 1
33.2 ± 0.14 (32–34) 17	13.0 ± 0.00 (13–13) 17	16.9 ± 0.12 (16–18) 17	16.8 ± 0.14 (16–18) 17	12.4 ± 0.13 (12–13) 16	12.6 ± 0.12 (12–13) 17	0.0 ± 0.00 (0–0) 17
34.0 ± 0.23 (33–35) 11	13.0 ± 0.00 (13–13) 11	16.6 ± 0.24 (15–17) 9	17.2 ± 0.18 (16–18) 11	12.5 ± 0.25 (11–14) 11	12.4 ± 0.20 (11–13) 11	0.0 ± 0.00 (0–0) 11
33.0 (33–33) 2	13.0 (13–13) 2	16.0 (16–16) 2	17.0 (17–17) 2	11.5 (11–12) 2	11.0 (11–11) 2	6.0 (5–7) 2
32.8 (32–33) 8	13.0 (13–13) 8	17.6 (17–18) 7	17.6 (17–18) 8	13.8 (13–14) 7	13.4 (12–14) 8	0.0 (0–0) 8
33.0 (33–33) 3	13.0 (13–13) 3	17.0 (17–17) 2	16.7 (15–18) 3	13.7 (13–14) 3	13.0 (12–14) 3	0.0 (0–0) 3
33.0 (33–33) 2	13.0 (13–13) 2	16.5 (16–17) 2	16.5 (16–17) 2	11.5 (11–12) 2	11.5 (11–12) 2	9.0 (8–10) 2
35.1 ± 0.23 (33–36) 12	13.0 ± 0.00 (13–13) 12	16.6 ± 0.24 (15–18) 11	16.6 ± 0.20 (16–18) 11	11.7 ± 0.26 (11–13) 10	11.6 ± 0.24 (11–13) 11	0.0 ± 0.00 (0–0) 12
32.5 ± 0.16 (32–33) 11	13.0 ± 0.00 (13–13) 11	16.7 ± 0.21 (16–18) 10	16.4 ± 0.25 (15–18) 11	11.7 ± 0.24 (11–13) 9	11.7 ± 0.17 (11–12) 9	6.7 (6–8) 7
35.8 (35–37) 4	13.0 (13–13) 6	16.7 (15–19) 6	16.8 (15–18) 6	11.8 (11–13) 5	12.2 (11–13) 6	0.0 (0–0) 6
33.2 (32–34) 5	13.2 (13–14) 5	16.8 (16–18) 4	16.8 (16–18) 5	12.2 (11–13) 5	12.4 (12–13) 5	8.5 (6–10) 4
35.0 (34–36) 5	13.8 (13–15) 5	16.0 (15–17) 4	16.0 (15–17) 4	11.7 (11–12) 3	12.0 (12–12) 3	0.0 (0–0) 5

TABLE 3
Continued

Species	Sample	Sex	Body length	Supralabials	Infralabials	Gulars	Ventrals
G. speciosus	Trinidad; T	♂	29.7 (26–33) 7	16.0 (16–16) 7	7.6 (7–8) 7	9.7 (9–10) 7	22.7 (22–24) 7
G. speciosus	Venezuela; U	♀	33.1 ± 1.54 (24–44) 16	15.9 ± 0.08 (15–16) 13	7.8 ± 0.12 (7–8) 13	9.3 ± 0.16 (8–10) 15	25.6 ± 0.34 (23–27) 14
G. speciosus	Venezuela; U	♂	31.8 ± 1.10 (22–39) 18	15.9 ± 0.06 (15–16) 16	7.9 ± 0.07 (7–8) 15	9.6 ± 0.16 (9–11) 16	23.3 ± 0.27 (22–25) 15
G. lineatus	Antilles; V	♀	32.5 (32–33) 2	16.0 (16–16) 2	8.0 (8–8) 2	11.0 (11–11) 2	27.5 (27–28) 2
G. lineatus	Antilles; V	♂	35.5 (35–36) 2	16.0 (16–16) 2	8.0 (8–8) 2	10.0 (10–10) 2	24.5 (24–25) 2
G. pleei	Mart.; W	♀	35.7 ± 1.67 (25–51) 21	14.0 ± 0.05 (13–14) 21	6.0 ± 0.00 (6–6) 21	11.2 ± 0.17 (10–12) 20	26.6 ± 0.33 (24–29) 19
G. pleei	Mart.; W	♂	34.0 ± 0.93 (22–42) 23	14.0 ± 0.00 (14–14) 23	6.0 ± 0.00 (6–6) 23	11.4 ± 0.16 (10–13) 23	25.0 ± 0.27 (23–27) 22

[a] Mean ± 1 Standard Error of the mean (range) and sample size. Sample locality data are in the Appendix.
[b] Identification is tentative in the absence of karyotypic or electrophoretic data and with only one specimen in the sample.

of *G. pleei*); dorsal caudal scales smooth at base of unregenerated tail, keeled posterior to first one-third or one-quarter tail length (but keeled on base of tail of *G. pleei*); regenerated caudal scales keeled. In addition, these lizards generally have five or six supralabials counted to the posterior edge of the eye, excepting *G. pleei,* which usually has four (sometimes five).

Considering the 10 more variable characters (table 3; body length and nine scale counts), no populations compared are distinctive for two of the characters (body length; number of finger lamellae), except females of *G. pleei* get larger than the others. *Gymnophthalmus pleei* is distinct from *G. underwoodi* and *G. speciosus* in seven characters (total number of supralabials; total number of infralabials counted to posterior edge of eye; number of gulars; number of ventrals; number of scales around midbody; number of toe lamellae; and number of femoral pores in males). *Gymnophthalmus lineatus* appears to be distinct from *G. underwoodi* and *G. speciosus* in five characters (gulars; ventrals; dorsals; scales around midbody; femoral pores in males). These data also are consistent with eliminating *pleei* and *lineatus* from the list of potential ancestors of *underwoodi.* Two of the three remaining species in the genus, *G. rubricaudus* (of central Argentina to northern Bolivia east of the Andes) and *G. multiscutatus* (of eastern Brazil in Bahia, Ceara, and Pernambuco) are ruled out on morphological and geographic grounds: both have distinctive scale characters and several strongly contrasting light stripes on a dark ground color.

Considering the more variable characters (table 3), the females of *G. underwoodi* and those of *G. speciosus* differ significantly (but with overlap) only in two characters (ventrals, higher in *speciosus*; dorsals, higher in *speciosus*); and in some samples of *speciosus* (not all) the number of scales around midbody averages one (or less) scale more than in *underwoodi.* These species are exceedingly similar in characters of size and scutellation, particularly considering the correlation in ventrals and dorsals of females (see multivariate analyses below). Based on all these observations, we suggest that the second (unknown) ancestor of *G. underwoodi* is similar to both *G. underwoodi* and *G. speciosus* but has, on average, fewer ventrals and dorsals.

One sample that is distinctive among all the unisexual samples is that from Ilha de Maraca, Roraima, northern Brazil (table 3, sample M). All eight of these specimens have

TABLE 3
Continued

Dorsals	Scales around midbody	Left toe lamellae	Right toe lamellae	Left finger lamellae	Right finger lamellae	Femoral pores
32.4 (31–34) 7	13.6 (13–15) 7	16.7 (16–18) 7	16.8 (15–18) 7	12.0 (11–13) 7	12.1 (11–13) 7	8.0 (4–10) 7
35.5 ± 0.49 (31–38) 13	14.0 ± 0.32 (13–17) 15	16.0 ± 0.48 (14–20) 14	16.2 ± 0.58 (14–20) 13	12.0 ± 0.44 (10–15) 13	11.5 ± 0.42 (10–15) 13	0.0 ± 0.00 (0–0) 13
32.6 ± 0.20 (31–34) 16	13.6 ± 0.34 (12–18) 17	16.3 ± 0.40 (14–20) 13	16.2 ± 0.34 (14–20) 15	11.7 ± 0.27 (11–15) 15	11.8 ± 0.36 (11–16) 14	8.5 ± 0.42 (6–13) 15
36.5 (36–37) 2	15.0 (15–15) 2	17.0 (17–17) 2	17.5 (17–18) 2	12.5 (12–13) 2	— —	0.0 (0–0) 2
35.0 (35–35) 2	14.5 (14–15) 2	17.5 (17–18) 2	16.0 (16–16) 2	12.5 (12–13) 2	12.0 (11–13) 2	10.0 (10–10) 2
33.3 ± 0.13 (32–34) 19	17.8 ± 0.22 (17–19) 21	19.2 ± 0.26 (17–21) 20	19.2 ± 0.28 (17–21) 19	12.6 ± 0.21 (11–15) 20	12.8 ± 0.17 (12–14) 18	0.0 ± 0.00 (0–0) 20
31.3 ± 0.13 (30–33) 23	17.6 ± 0.20 (16–19) 23	18.4 ± 0.19 (17–20) 21	18.7 ± 0.23 (17–21) 21	13.0 ± 0.20 (12–15) 23	13.2 ± 0.19 (12–15) 22	13.4 ± 0.31 (11–16) 22

six infralabials (three on each side) to the posterior edge of the eye; the second on each side is elongate. These lizards also more frequently have a second loreal on one side and the nare low in the nasal, suggesting that they need additional investigation. They could represent a distinctive clone of *G. underwoodi* or they could be a different species. Most lizards in sample Q have infralabials similar to these also.

Given the difficulties of distinguishing between *G. underwoodi* and *G. speciosus* on the basis of morphology of preserved specimens, we should explain the identifications presented in table 3. For *underwoodi*, karyotypic and/or electrophoretic data were available for samples D, H, J, and L, and all were identical. Other samples identified here as *underwoodi* are morphologically similar or indistinguishable and also lack males. The sample of MZUSP females from eastern Suriname (Z) might include both *underwoodi* and *speciosus* because two MZUSP males (sample P) have the same locality data; it is conceivable that sample Q includes both species also (P and Q include the males identified by Vanzolini, 1976, as *G. underwoodi*). For *speciosus*, karyotypic and/or electrophoretic data were available only for sample T; other samples identified as *speciosus* are morphologically similar or indistinguishable and include males also. This includes the MPEG specimens (sample R) from Colonia Coronel Mota, Roraima, Brazil, with a 50:50 sex ratio, originally identified by Cunha (1981) as *G. underwoodi*. We follow Hoogmoed (1973) in applying the name *speciosus* to bisexual populations in northern South America, realizing that future comparisons may reveal that additional cryptic species are involved (the type locality for *G. speciosus* is Nicaragua).

Multivariate Morphological Analyses

Because significant sexual dimorphism is indicated for three characters (females have more ventrals than males, more dorsals, but no femoral pores; table 3), principal components analyses (PCAs) were performed separately on males and females. Several different PCAs were performed for various reasons, based on the same 10 characters (nine for females) in table 3, and these are discussed separately below.

PCA 1: The 53 males of *G. speciosus*, *G. lineatus*, and *G. pleei* with complete data were analyzed to see whether clustering would be consistent with recognizing three or more

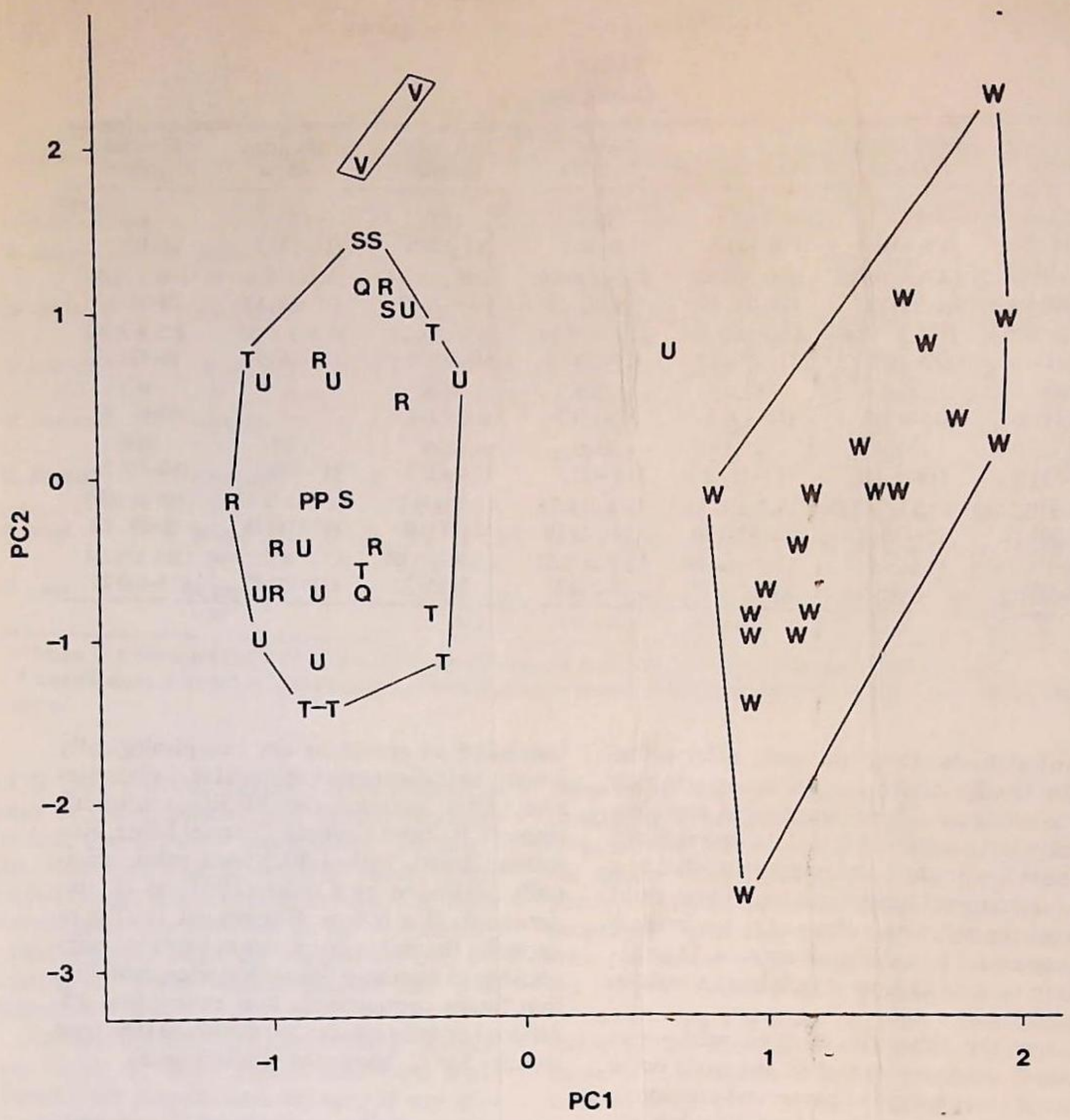

Fig. 4. Polygons and letters indicating scores of 53 malesof *Gymnophthalmus* (*lineatus, pleei, speciosus*) on the first two principal components extracted from te correlation matrix of 10 morphological characters (tables 3, 4). Each letter represents an individualfrom samples listed with corresponding letters in table 3. The distinctive *speciosus* (individual U) is UIMNH 63577 from "Venezuela."

taxa. Assuming that the *pleei* specimens from the island of Martinique represent one species, would PCA show the *speciosus* to have a similar form of clustering (even if occupying a different polygon), or might the *speciosus* occur in two clusters that could represent unrecognized cryptic species? The analysis (fig. 4) reveled three groups consistent with the knowntaxa, but one specimen of *speciosus* (an individual of sample U, UIMNH 63577, with locality data specific only to "Venezuela") was separated from the other *speciosus* specimns on the first principal component (PC1).The *pleei* (W) completely separated

TABLE 4
Character Loadings on First Two Axes for Three Principal Components Analyses of *Gymnophthalmus* Morphology[a]

Character	PCA 1		PCA 2		PCA 3	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
Body length	0.384	0.732	0.170	−0.100	−0.074	−0.481
Supralabials	−0.915	0.156	−0.924	0.062	−0.135	0.565
Infralabials	−0.908	0.254	−0.762	0.212	0.171	0.760
Gulars	0.845	0.081	0.721	0.023	0.067	0.358
Ventrals	0.738	0.424	0.722	0.541	0.819	−0.196
Dorsals	−0.654	0.533	0.060	0.832	0.801	−0.043
Around body	0.906	−0.101	0.947	−0.010	0.314	−0.284
Toe lamellae	0.814	−0.165	0.591	−0.535	−0.617	−0.077
Finger lamellae	0.713	0.271	−0.130	−0.801	−0.796	−0.154
Pores	0.897	0.102	—	—	—	—
Variation expl.	63%	12%	42%	22%	28%	16%

[a] Based on data summarized in table 3.

from the other taxa on PC1, the form of clustering in *pleei* and *speciosus* (P-U) was similar, and *lineatus* (V) was separated from *speciosus* on PC2; however, the sample size of *lineatus* was small. For *speciosus,* samples R (Colonia Coronel Mota, Brazil) and T (Chacachacare Island, Republic of Trinidad and Tobago) are particularly informative because they each represent samples of one deme and we also have karyotypic and electrophoretic data for sample T; R and T cluster together (fig. 4). The correlation matrix showed significant correlation among all scale counts except ventrals and dorsals for this comparison, but little correlation between body length and the scale counts. The first two principal components jointly accounted for 75 percent of the total variation in the data set (PC1 = 63%; PC2 = 12%), and no other principal components explained as much as 10 percent. The loadings on the components are listed in table 4 and the scores are shown in figure 4.

PCA 2: The 255 females of *G. speciosus, G. lineatus, G. pleei,* and *G. underwoodi* with complete data were analyzed to see whether clustering would be consistent with recognizing four or more taxa and to see if the females cluster similarly to the males. Would the females of *speciosus* have a form of clustering similar to the females of *pleei* from Martinique (even if occupying a different polygon), or might the *speciosus* females occur in two clusters that could represent unrecognized cryptic species? The analysis (fig. 5) revealed that *pleei* (W) completely separated from the others on PC1; most *speciosus* specimens (R-U) clustered reasonably well together (but one individual of U, FMNH 176692 from Puerto Ayacucho, Amazonas, Venezuela, was clearly distinct on PC2); *lineatus* (V) was separated from *speciosus* on PC1, although there may have been overlap if there had been a larger sample of *lineatus*; and the positively identified *underwoodi* (HEJO polygon) tended to separate from the positively identified *speciosus,* with some overlap of their polygons. Again, the most informative *speciosus* samples, R and T, clustered together, as in the males. The most informative *underwoodi,* each representing restricted localities and represented by karyotypic and/or electrophoretic data, are D (Trinidad) and H, J, and L (Suriname); these clustered together and with A (Barbados; type locality). All 11 individuals of Q and M with complete data clustered together and separate from the others, again indicating that these Brazilian populations need additional study. Other individuals of interest are K and F (table 3, fig. 5), which could be either *underwoodi* or *speciosus,* and one Z (MZUSP 11593), which clustered with the *speciosus* (Z is the sample from Langamankondre, Suriname, that included two males; see below). The correlation matrix showed significant correlation among most

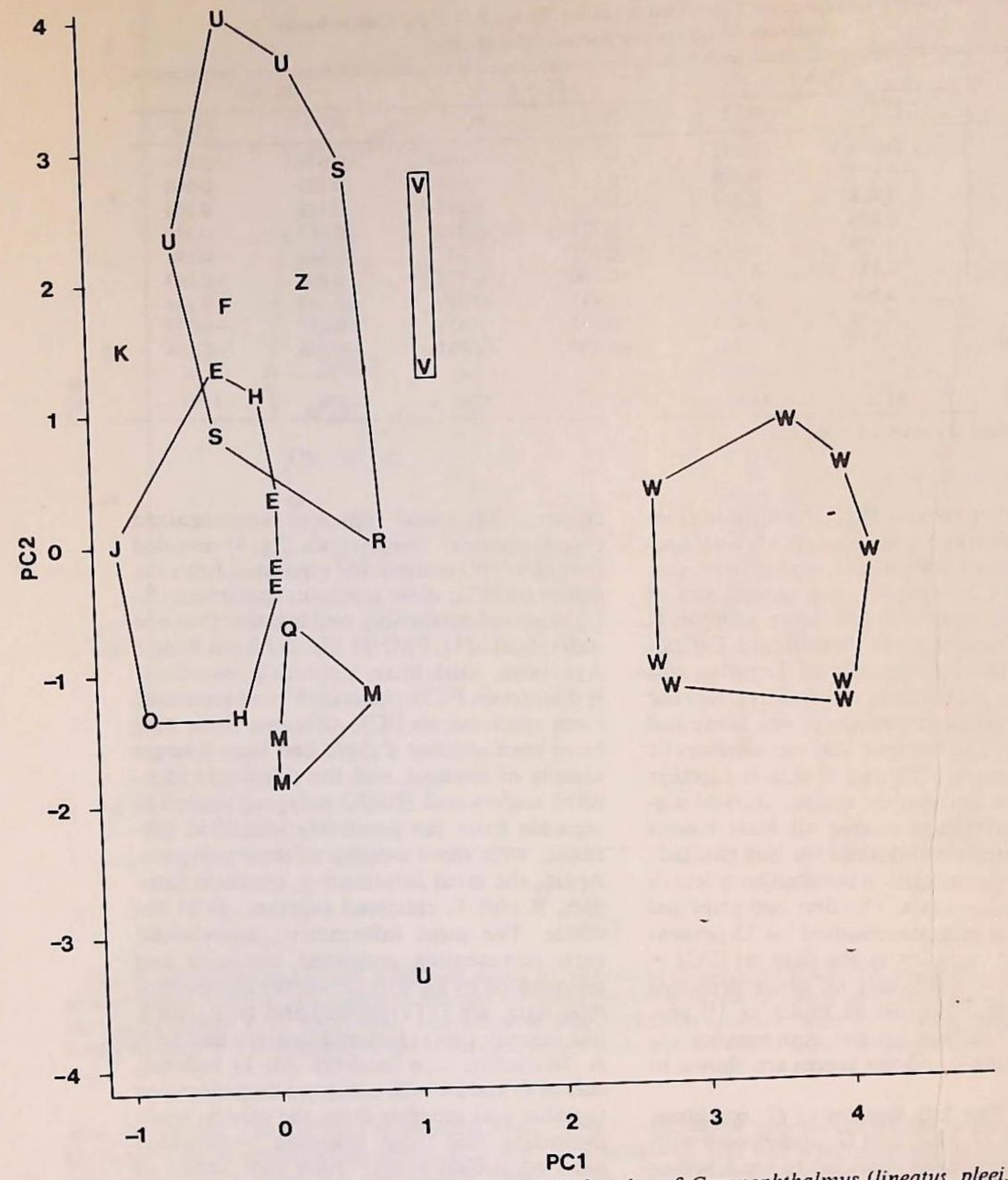

Fig. 5. Polygons and letters indicating scores of 255 females of *Gymnophthalmus* (*lineatus, pleei, speciosus, underwoodi*) on the first two principal components extracted from the correlation matrix of nine morphological characters (tables 3, 4). Only letters for individuals on the periphery of each polygon are shown (due to crowding), correlated with samples listed in table 3. Sample sizes are as follows: *lineatus* (V), 2; *pleei* (W), 17; *speciosus* (USR polygon), 29, including 3 from sample T, 11 from R; Q and M polygon, 11; and *underwoodi* (HEJO polygon), 196, including 32 for sample A (type locality, Barbados), 40 for D, 10 for H, 9 for J, 17 for L, and 11 for Z. The distinctive individual *speciosus* indicated (U) is FMNH 176692 from Puerto Ayacucho, Amazonas, Venezuela.

of the scale counts, including ventrals and dorsals, but no correlation between body length and the scale counts. The first two principal components jointly accounted for 64 percent of the total variation in the data set (PC1 = 42%; PC2 = 22%), PC3 accounted for 11 percent, and no other principal component explained as much as 10 percent. The loadings on the components are listed in table 4.

PCA 3: Samples of *G. lineatus* and *G. pleei* were included in the previous analyses to compare patterns of clustering within *G. speciosus* and *G. underwoodi* with samples of bisexual species from limited geographic areas. Our purpose now, however, is to compare clustering among the *underwoodi,* the *speciosus,* and the samples of uncertain identity more directly (table 3) to see if the unisexual samples cluster with subsets of the bisexuals in a way suggesting that two cryptic ancestors of the *underwoodi* are represented among these specimens. Since *pleei* and *lineatus* are not considered as ancestors, removing them from this analysis prevents their characters from distorting the spatial arrangements among the specimens on which we focus now. Thus, the 236 females of *G. speciosus, G. underwoodi,* and *Gymnophthalmus* of uncertain identity (table 3) with complete data were analyzed. The analysis (fig. 6) revealed that the *speciosus* specimens clustered together reasonably well (again, an individual U, FMNH 176692 from Puerto Ayacucho, Venezuela, was distinct, this time on PC1), and the positively identified *underwoodi* tended to separate from the *speciosus,* but their polygons did overlap. Again, the most informative *speciosus* samples, R and T, clustered together, and the most informative *underwoodi* samples (A, D, H, J, and L) clustered together also. Again, all 11 specimens of Q and M clustered together but separately from the others. This time, specimen K clustered ambiguously with *speciosus* and *underwoodi,* but the one F and MZUSP 11593 (of sample Z) clustered with the *speciosus,* as in PCA 2. Spatial arrangement of the clusters (fig. 6) is not such that *underwoodi* occupies a sector intermediate to two others, although the identity of FMNH 176692 is questionable if it is not an aberrant individual. The correlation matrix showed significant correlation among many scale counts, including ventrals and dorsals, but no correlation between body length and the scale counts. The first two principal components jointly accounted for only 44 percent of the total variation in the data set (PC1 = 28%; PC2 = 16%), PC3 and PC4 each accounted for 12 percent, and no other principal component explained as much as 10 percent. The loadings on the components are listed in table 4. As suggested by the univariate comparisons (see above; table 3), PCA 3 (fig. 6; table 4) suggests that the second bisexual ancestor of *G. underwoodi* has, on average, fewer ventrals and dorsals than *underwoodi* or *G. speciosus.*

Coloration

In colors and color pattern, females of *G. underwoodi* and *G. speciosus* are exceedingly similar, whereas *G. pleei* and the other known species of *Gymnophthalmus* are more distinct. In life, the character that may be most useful for distinguishing the cryptic species is color of the tail. General form and pattern of living lizards are shown in figure 7.

The following color notes on *G. underwoodi* are based on living females from the Emperor Valley Zoo, Port-of-Spain, Trinidad (AMNH 119742–119743 and 128446–128449); from Christiaankondre, Suriname (AMNH 133314–133321); and from Lelydorp, Suriname (AMNH 133329 and 133333). Dorsum medium brown with tiny black specks and inconspicuous copper iridescence; light tan dorsolateral stripe from snout passing over eye, fading near midbody (offset anteriorly on body, above and below, by adjacent row of black dots), evident weakly over hips; sides, arms, hands, legs, feet uniform dark brown, rarely with tiny metallic copper flecks on flanks; top of head medium brown; base of tail medium brown, encircled with tan and black dots; distal half of tail gray (regenerated tail brown or gray); chin, throat, chest, undersides of arms, abdomen gray with copper iridescence (yellow iridescence in juveniles) and tiny black flecks; undersides of legs, anal region, tail grayish-brown, but often tail very light gray.

The following color notes on *G. speciosus* are based on living individuals from Cha-

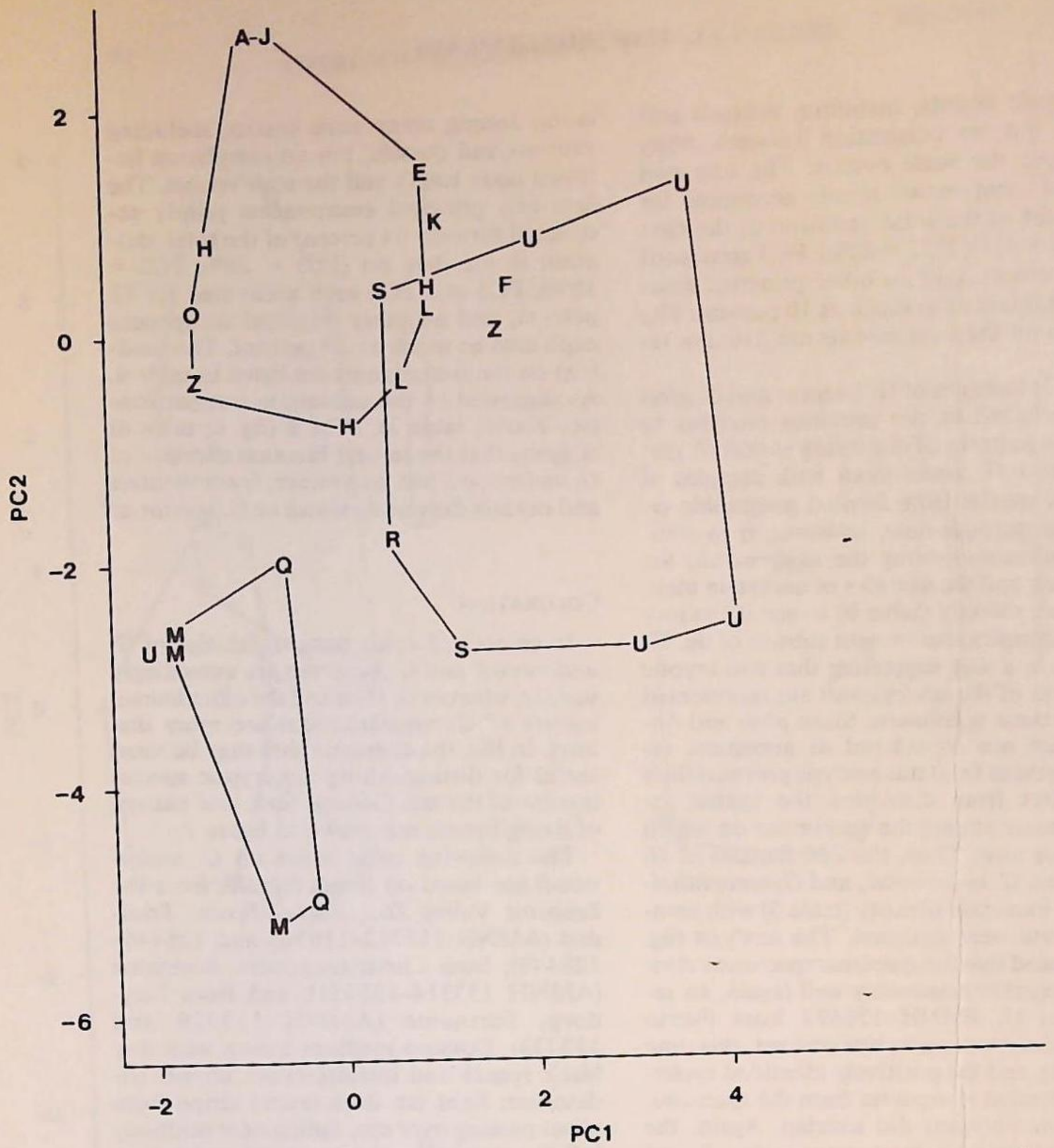

Fig. 6. Polygons and letters indicating scores of 236 females of *Gymnophthalmus* (*speciosus, underwoodi*) on the first two principal components extracted from the correlation matrix of nine morphological characters (tables 3, 4). Individuals analyzed and included in the respective polygons are the same ones as in figure 5, except the *G. pleei* (W) and *G. lineatus* (V) were excluded. The distinctive individual *speciosus* indicated (U) is FMNH 176692 from Puerto Ayacucho, Amazonas, Venezuela.

cachacare Island, Republic of Trinidad and Tobago (AMNH 119744 and 128438–128445). These animals appeared to be identical to the *G. underwoodi* noted above but with the following few differences, some of which are slight: dorsum with or without subtle, small dark brown and tan flecks in longitudinal rows; flanks usually with flecks of

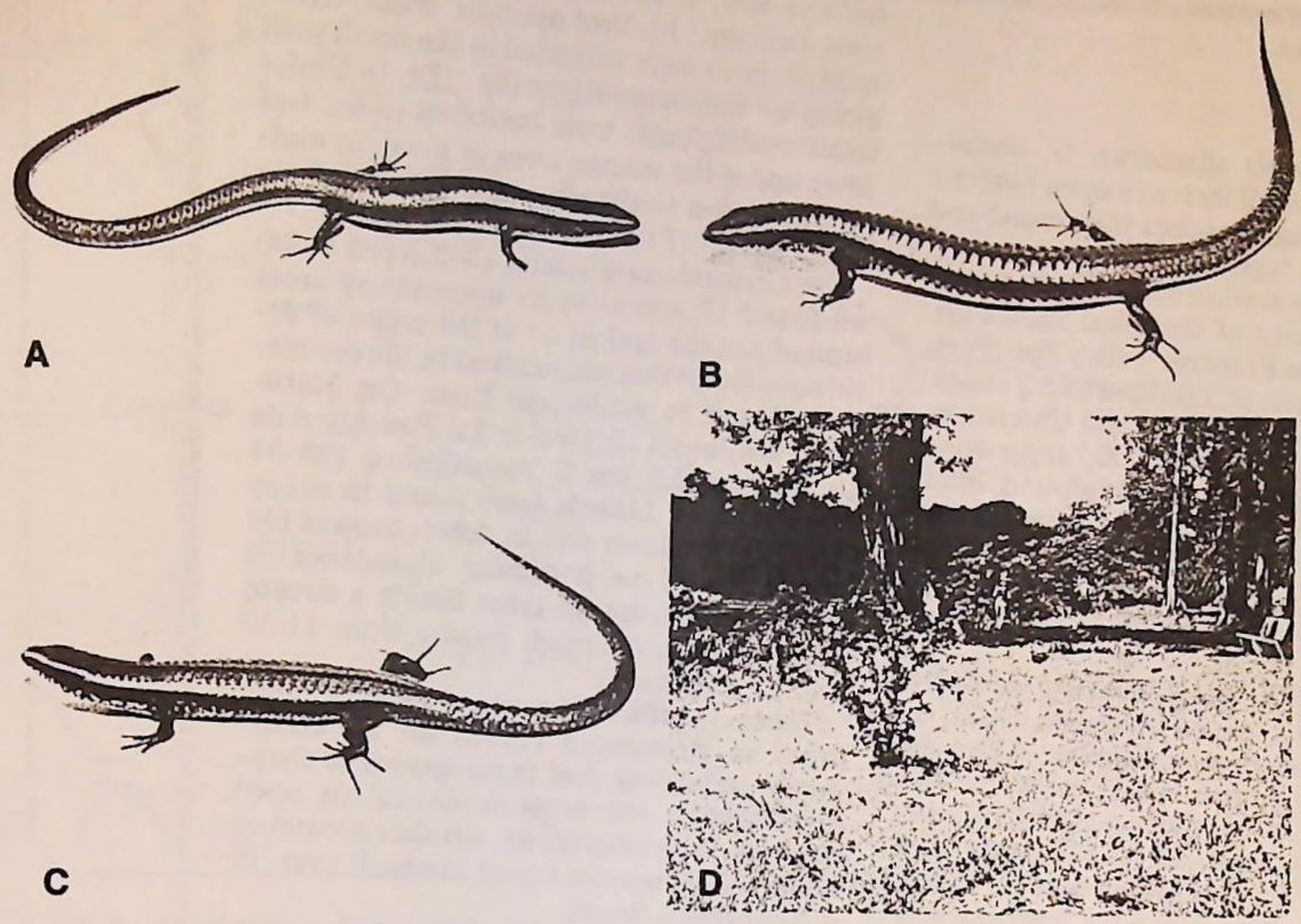

Fig. 7. **A.** *Gymnophthalmus underwoodi* (AMNH 119415) from Brokopondo, Suriname (snout-vent length, 32 mm). **B.** *Gymnophthalmus speciosus* (from series of AMNH 128438–128445) from Chacachacare Island, Republic of Trinidad and Tobago. **C.** *Gymnophthalmus pleei* (from series of AMNH 128431–128437) from Martinique. **D.** Open riverside habitat (along Suriname River) of *G. underwoodi* in Brokopondo, Suriname, 2 July 1980.

metallic copper; light tan dorsolateral stripe continuing along body (sometimes as row of spots, posteriorly) onto base of tail, there breaking up into series of tan spots; on some, lateral scales edged with beige or having an inconspicuous light line (ear to hind leg), perhaps broken; regenerated tail brown; undersides of chin, throat, arms, chest, abdomen bright pinkish-orange or copper; underside of legs gray, of tail pinkish-copper or orangish-tan (gray distally). The only difference between *G. underwoodi* and *G. speciosus* clearly recognized in specimens that have been in preservative for several years is the continuation of the dorsolateral light line to the base of the tail (usually seen as a row of light spots) in *speciosus* and, in some *speciosus*, the less conspicuous lateral line (most often visible on neck). The similarity in coloration of these species is consistent with the genetic data suggesting that *speciosus* is one of the bisexual ancestors of *underwoodi* and consistent with suggesting that the other ancestor also is morphologically similar to these two.

Gymnophthalmus pleei is similar in coloration also, as shown by notes on living individuals from Martinique (AMNH 128423–128437). These appeared to be identical to the *G. underwoodi* noted above but with the following differences: vertebral area with poorly defined brown stripe; series of black flecks along upper edge of dorsolateral light stripes; pale copper and gold flecks on sides anterior to arms; arms of adults with pale copper and gold stripes and flecks; top of head and tail base with black specks; chin, throat,

chest, abdomen with more conspicuous dark gray or black flecks.

Ecology

Gymnophthalmus speciosus, G. underwoodi, and *G. pleei* all thrive in open habitats where direct sunlight reaches the ground and temperatures are high (fig. 7D).

At the research station Simla (Arima Valley), the University of the West Indies (St. Augustin), and the Emperor Valley Zoo (Port-of-Spain), Republic of Trinidad and Tobago, and at Brokopondo (fig. 7D) and Christiaankondre, Suriname, we found *G. underwoodi* active only on hot, open, sunlit ground, often around buildings. Individuals are best caught in areas of short grass, including lawns, because they are small, they skitter about quickly, and they dive into litter and holes for cover.

Populations can be particularly dense in areas where walls, paved walkways, rocks, or leaf litter provide extra protection. Although other teiids are more active earlier in the morning, the major activity period for *G. underwoodi* was from about 10:30 A.M. to 2:00 P.M. on clear, sunny days in March, April, June, and July. The following temperatures (degrees centigrade) were recorded in Brokopondo at sites where lizards were captured from 30 June to 2 July 1980: air (1 m above ground), 30.3, substrate, 32.0, air among grass (1 cm above ground) where the lizard ran, 34.2 (10:30 A.M.); air (1 m above ground), 29.6, substrate, 32.2 (11:40 A.M.); air (1 m above ground), 30.6, substrate, 38.8, air among grass (1 cm above ground) where the lizard ran, 33.4 (12:40 P.M.). Immediately after recording the last series of temperatures, we stepped into adjacent forest and recorded the following temperatures about 5 m away: air (1 m above ground), 30.1, substrate, 26.5, and air among vegetation (1 cm above ground), 27.7. We did not see *G. underwoodi* in forest habitat, although several open areas in which we saw the lizards were adjacent to forest. The hottest site at which we saw a *G. underwoodi* lizard was a pile of rocks in full sunlight at 2:00 P.M. in Brokopondo. The rocks were so hot that one could not grasp them and the air temperature where the lizard disappeared among them was 40.0°C. On relatively cool, partly cloudy days with intermittent sun, a few *Gymnophthalmus* were seen basking. In Brokopondo, most *Gymnophthalmus* were collected in the small park along the Suriname River (fig. 7D). In Christiaankondre, most were collected in the leaf litter under the mango trees in town, in midafternoon, on sunlit ground at the periphery of the shade of the trees.

On Chacachacare Island (3–5 April 1984) we found *G. speciosus* in open sunny areas around houses and in or at the edges of deciduous forest that was leafless in the dry season, always in sunlit leaf litter. On Martinique we found *G. pleei* at La Plantation de La Leyritz, 2.5 km S Basse-Pointe (28–31 March 1984). Lizards were found in sunny places on the lawn and in debris around old buildings and in particular abundance in bamboo leaf litter on grass beside a stream near the entrance road, mostly from 11:30 A.M. to 4:00 P.M.

These habitat notes are consistent with those of Hoogmoed (1973) for *G. underwoodi,* indicating that these species of *Gymnophthalmus* are most successful in open habitats, such as savanna, whether natural or disturbed. They are found rarely, if ever, in full-canopied forest.

The Missing Ancestor

All of the morphological, karyotypic, and biochemical data presented above are consistent with the conclusion that the unisexual *G. underwoodi* had a hybrid origin. *Gymnophthalmus speciosus* has a combination of traits (genetic, morphological, ecological, distributional) that strongly suggest it was one of the bisexual ancestors. *Gymnophthalmus pleei* is ruled out as the other bisexual ancestor based on external morphology, karyotypes, and proteins detected by electrophoresis. External morphology suggests that none of the other known species of *Gymnophthalmus* matches predictions for the other ancestor. We suggest that the other bisexual ancestor is a cryptic species morphologically similar to *G. underwoodi* and *G. speciosus,* which, similarly, lives in open habitats somewhere in or near the Guiana Region (northern Brazil, eastern Venezuela, Guyana, Surina-

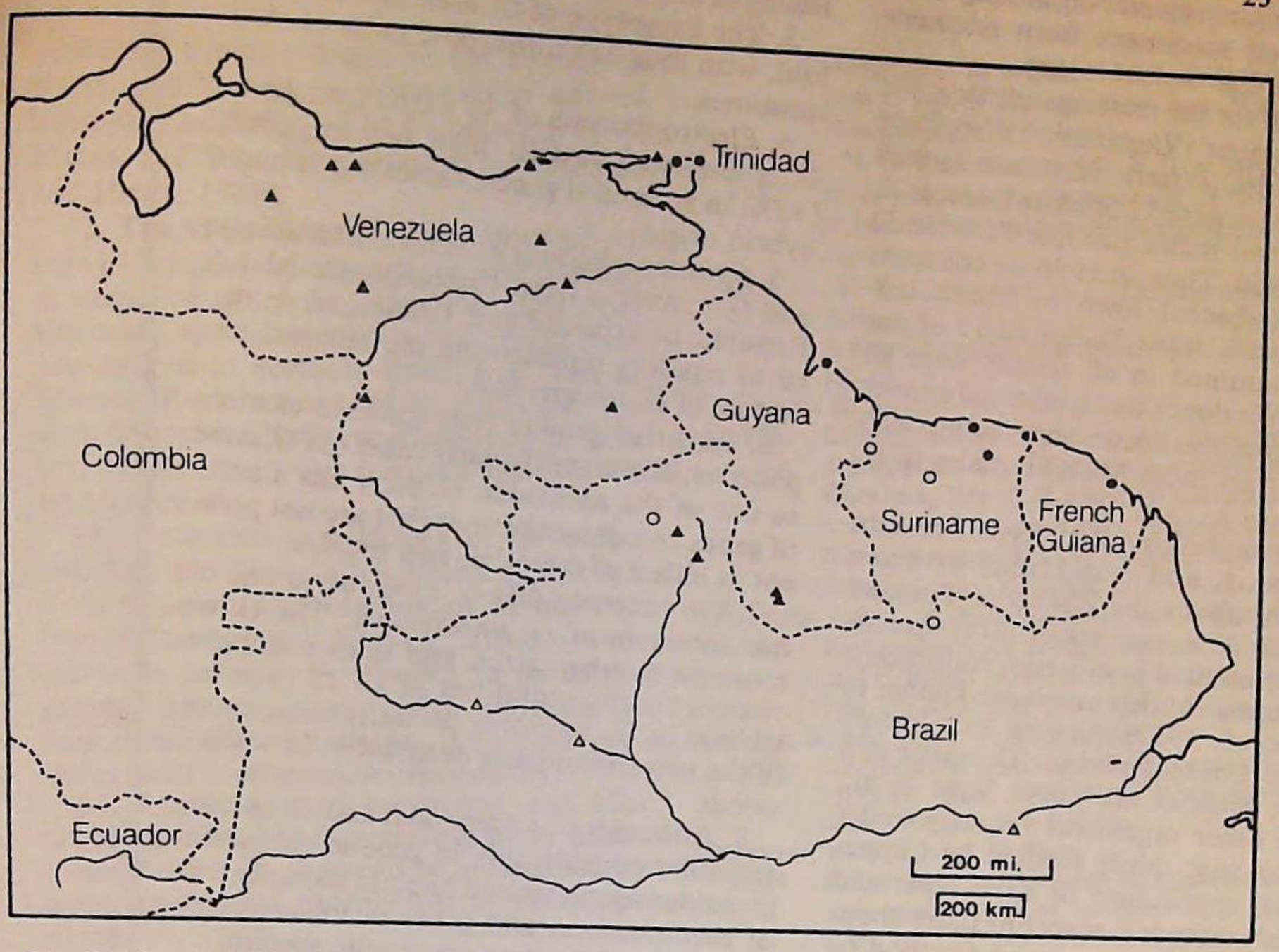

Fig. 8. Localities for *Gymnophthalmus* in the Guiana Region of northern South America and the Republic of Trinidad and Tobago. (●) *G. underwoodi*; (○) *G. underwoodi*?; (▲) *G. speciosus*; (△) *G.* ? (specimens referred to as such in table 3 and the Appendix). Localities of special interest are as follows: Puerto Ayacucho, Amazonas, Venezuela (solid triangle on border with Colombia); Chacachacare Island (solid triangle immediately to the west of northern Trinidad); Ilha de Maraca, Roraima, Brazil (open circle in northern Brazil); Orealla, Guyana (open circle on border with Suriname); Brokopondo, Suriname (southernmost solid circle in Suriname); and Langamankondre and Christiaankondre, Suriname (partial closed circle and partial closed triangle together on border with French Guiana, near the coast).

me, French Guiana; fig. 8) of northern South America.

The morphological analyses indicate that the unknown ancestor differs from *G. underwoodi* and *G. speciosus* by having, on average, somewhat fewer ventral and dorsal scales (tables 3, 4; fig. 6), and these are not independent characters. We also presented detailed predictions for the karyotype (fig. 2) and relative mobilities of proteins encoded by 33 gene loci (table 2; fig. 3) of this unknown bisexual ancestor.

Future samples that may represent this unknown ancestor should be tested karyotypically and electrophoretically. The karyotype alone would be highly suggestive, when compared with figure 2. For electrophoresis, the new samples would have to be run with at least one known *G. underwoodi* sample on the same gels, and then the results could be compared with ours (table 2; fig. 3). Ideally, future comparisons should include *G. speciosus* from the mainland and from the type locality of *speciosus* (Nicaragua) also, as our specimens of *speciosus* so tested were all from Chacachacare Island. Although the morphology, including principal components analyses (figs. 4–6), suggests that all or nearly all specimens we referred to *speciosus* represent one taxon, it is possible that the un-

known ancestor is masquerading among some of the preserved specimens from northern South America that we examined.

In our search for the missing ancestor, the MZUSP specimens (Vanzolini, 1976) from Langamankondre, eastern Suriname looked promising. There were 11 females (sample Z, table 3) and two males (sample P, table 3) collected in 1966. Thus, in 1986 we collected in the area (adjacent town of Christiaankondre; sample L, table 3), but all 17 of our specimens examined in all details were *G. underwoodi*. We doubt that a bisexual species of *Gymnophthalmus* occurs there today, and for now, we refer those MZUSP males to *G. speciosus*.

By using morphology, karyotypes, protein electrophoresis, and deduction, we have learned more about the unknown bisexual ancestor than is known about most species of lizards represented in museum collections, yet no specimens of this taxon are known to exist (Cole et al., 1989). As with teiid lizards of the genus *Cnemidophorus* (Dessauer and Cole, 1989; Sites et al., 1990; Vyas et al., 1990), and other organisms recently under investigation (e.g., birds studied by Cappanella, 1988), application of karyotypic and biochemical methods is revealing more about tropical diversity than can be understood by using traditional morphological characters alone.

SUMMARY, CONCLUSIONS, AND SCENARIO ON THE HYBRID ORIGIN OF *G. UNDERWOODI*

1. Morphological, karyotypic, and biochemical observations confirm that *Gymnophthalmus underwoodi* occurs in all-female populations in Trinidad and northern Suriname. Comparative morphology indicates that similar unisexual populations of *underwoodi* occur also in French Guiana, northern Brazil, Guyana, and the following islands of the West Indies: Barbados (type locality), Dominica, Grenada, Guadeloupe, and St. Vincent. Two specimens from St. Thomas probably represent an artificial introduction or erroneous locality data.

2. Females of *G. underwoodi* from Trinidad and Suriname produce clones independently by parthenogenetic reproduction (also see Hardy et al., 1989).

3. The karyotype of *G. underwoodi* is diploid, with four heteromorphic pairs of chromosomes.

4. Electrophoresis of 33 tissue proteins of *G. underwoodi* reveals high heterozygosity (45%) in structural genes, indicating it had a hybrid origin.

5. *Gymnophthalmus pleei* from Martinique and *G. speciosus* from Chacachacare Island, Republic of Trinidad and Tobago, were tested as possibly representing the bisexual ancestors of *G. underwoodi*.

6. Sensitive genetic tests (protein electrophoresis; karyotypes) clearly ruled out *G. pleei* as one of the ancestors; *G. pleei* has a suite of genes and chromosomes that are not present in either of the other two species.

7. We conclude that *G. speciosus* is one of the ancestors of *G. underwoodi*. The chromosome number, sizes, and shapes and the electrophoretic mobilities of all 33 proteins studied in *G. speciosus* perfectly match one of the two haploid sets detected in *G. underwoodi*.

8. Although *G. underwoodi* and *G. speciosus* differ considerably in genetic characters (considering the second haploid complement of chromosomes and genes in *underwoodi*), morphologically they are cryptic species.

9. The second bisexual ancestor of *G. underwoodi* remains to be found. We predict it is a third cryptic species similar to *underwoodi* and *speciosus* in morphology, ecology, and behavior, and living somewhere in or near the Güiana Region of northern South America.

10. Electrophoresis of tissue proteins and karyotypes from fresh samples would provide the critical tests for identifying the second bisexual ancestor. Detailed predictions are presented (above) for the morphology, karyotype, and electrophoretic mobilities of 33 proteins of this otherwise unknown ancestor.

11. The hybrid event creating *G. underwoodi* probably occurred in northern South America, associated with shifting habitats (savanna or other open habitats versus forest; Cole et al., 1989). Such habitat shifts accompany fluctuations in rainfall, as in Pleistocene

to Recent times, changes in the courses of rivers, and human modifications of natural habitats (e.g., Haffer, 1979; Hoogmoed, 1979; Huber, 1987; and several papers in Vanzolini and Heyer, 1988).

12. The same clone of *G. underwoodi* occurs in Trinidad and Suriname, and possibly at many or all of the other localities from which the species is known. Specimens from populations in northern Brazil (e.g., Ilha de Maraca, Roraima) should be tested for possible differences, however. There may be more cryptic species in this complex than we are now aware of.

13. Unisexual populations of *G. underwoodi* in the West Indies probably resulted from dispersal and colonization by one or a few parthenogenetic females. Island colonization is particularly efficient in parthenogenetic species; reproductive potential is enormous, as every normal individual produces female offspring independently.

14. Application of karyotypic and biochemical methods is revealing more about tropical diversity than can be understood by using traditional morphological characters alone.

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